Description, Calibration, and Sensitivity Analysis of the Local Ecosystem Submodel of a Global Model of Carbon and Nitrogen Cycling and the Water Balance in the Terrestrial Biosphere

J.R. Kercher
J.Q. Chambers

October 1995

Lawrence Livermore National Laboratory

Description, Calibration, and Sensitivity Analysis of the Local Ecosystem
Submodel of a Global Model of Carbon and Nitrogen Cycling and the Water
Balance in the Terrestrial Biosphere

J.R. Kercher[1] and J.Q. Chambers[2,3]

[1]Health and Ecological Assessment Division, L-256

[2]Global Climate Research Division, L-256

Lawrence Livermore National Laboratory,

Livermore, California 94550

and

[3]Department of Biological Sciences

University of California

Santa Barbara, California 93106

ABSTRACT

We have developed a geographically-distributed ecosystem model for the carbon, nitrogen, and water dynamics of the terrestrial biosphere TERRA. The local ecosystem model of TERRA consists of coupled, modified versions of TEM and DAYTRANS. The ecosystem model in each grid cell calculates water fluxes of evaporation, transpiration, and runoff; carbon fluxes of gross primary productivity, litterfall, and plant and soil respiration; and nitrogen fluxes of vegetation uptake, litterfall, mineralization, immobilization, and system loss. The state variables are soil water content; carbon in live vegetation; carbon in soil; nitrogen in live vegetation; organic nitrogen in soil and litter; available inorganic nitrogen aggregating nitrites, nitrates, and ammonia; and a variable for allocation. Carbon and nitrogen dynamics are calibrated to specific sites in 17 vegetation types. Eight parameters are determined during calibration for each of the 17 vegetation types. At calibration, the annual average values of carbon in vegetation C_v show site differences that derive from the vegetation-type specific parameters and intersite variation in climate and soils. From calibration, we recover the average C_v of forests, woodlands, savannas, grasslands, shrublands, and tundra that were used to develop the model initially. The timing of the phases of the annual variation is driven by temperature and light in the high latitude and moist temperate zones. The dry temperate zones are driven by temperature, precipitation, and light. In the tropics, precipitation is the key variable in annual variation. The seasonal responses are even more clearly demonstrated in net primary production and show the same controlling factors.

We have found the sensitivities of the total ecosystem, total carbon storage, and net primary production to changes in model parameters. With only a few exceptions, the systems are ultra sensitive to the parameters controlling the effect of soil moisture on soil decomposition and soil respiration from the tundra to the tropics. The calibration parameters are important in all 17 vegetation types in determining the total system sensitivity; of these, usually K_d (parameter for soil respiration) is the most important and K_r (parameter for plant respiration), the least. The most common ordering in total system sensitivity for the eight calibration parameters is K_d, N_{loss} (loss of nitrogen from soil), K_{fall} (rate of carbon transfer by litterfall), N_{max} (rate of nitrogen uptake by vegetation), C_{max} (gross primary productivity), L_{nc} (nitrogen transfer by litterfall), N_{up} (immobilization of nitrogen by bacteria in litter), and K_r, from the most sensitive to the least. This suggests that immobilization and plant respiration are less important on a relative basis for the total system, and soil respiration and nitrogen losses from soils are the most important processes. The parameter that controls the respiration response to temperature Q_{10} is a key parameter in total system sensitivity, total carbon sequestration and net primary productivity in all systems except for the high latitudes. Colder systems were found to be sensitive to more parameters than the others suggesting that these systems may be somewhat more fragile than their neighbors in more temperate climates.

We examined the response of total stored carbon in vegetation and soils and net primary productivity to changes in environmental variables of nitrogen inputs, temperature, atmospheric CO_2 level, precipitation, dewpoint, and hours of sunshine. For a 1°C temperature increase most systems (except high latitude, cold systems) experience a net loss in carbon. However, a rise of 2°C is enough to force even the coldest system into a net loss of stored carbon. Raising the dewpoint lowers the vapor pressure deficit and increases carbon storage for all systems except the tundras and boreal woodland. For a 1° and 2°C temperature increase, the multiple processes in which temperature plays a role combine for most high latitude and temperate systems to produce a net gain in net primary productivity at steady state. Most low latitude systems show a net decrease in net primary productivity as temperature rises. The TERRA model exhibited a fertilization response to increases in nitrogen inputs. A 10% increase in nitrogen deposition produced about a 2.3±0.9% increase in carbon sequestration averaged over the 17 systems. More

importantly it was found that on the basis of a fixed amount applied, there was substantial difference across the systems with the tundra, boreal, and temperate evergreen forests sequestering over 10^4 gC at steady state for every gram of nitrogen added per year. These results suggest that increased nitrogen inputs to the terrestrial biosphere might be an important factor in carbon sequestration. The model results suggest that any future increases in precipitation will have the net effect of increasing carbon storage in most systems. Doubling CO_2 by itself produces about a 12±2% increase in carbon storage averaged across all 17 systems. This increase is actually greater for some systems (usually the colder systems) under a concomitant temperature rise. All other systems, especially in the tropics show a marked decrease with temperature in the amount by which carbon storage is enhanced under a CO_2 doubling. The systems that experience a sequestration effect for increases in both temperature and CO_2 are cold systems with nutrient limitations. These systems experienced an increase in productivity (at least in part) due to a speed up of the release of nitrogen by soil decomposition. Changing the temperature can affect the decomposition rate in the soil and the release (mineralization) of nitrogen by decomposition and also the immobilization rate. These changes alter the availability of nitrogen to the plant and can result in a fertilization effect for increasing temperature.

INTRODUCTION

Two important, related problems in the study of the global terrestrial biosphere are the prediction of the global biogeochemical cycling of carbon and the effect of climate change on global terrestrial production.

The first problem is important to solve in order to predict future levels of atmospheric CO_2. The level of CO_2 is one of the precursors for predicting climate change given the current state-of-the-art in general circulation modeling. Future levels of CO_2 will depend on the global carbon cycle and possible sequestration of carbon in terrestrial or oceanic pools. Preindustrial levels of CO_2 were about 590 gigatons of carbon (10^{15} gC) (or about 280 ppmv) (Neftel et al. 1985) and by 1988 had risen to about 740 Gt C (or about 350 ppmv) (Keeling et al. 1989). Keeling (1973) and Marland et al. (1989) estimate that emissions from fossil fuel burning were about 200 GtC during that period. For that same period, Houghton et al. (1989) estimated that 90 to 120 GtC were released from the terrestrial biosphere by land use changes. Thus roughly half the total estimated emissions remain in the atmosphere. The balance has gone into either ocean pools or terrestrial pools. Resolving where this carbon has gone and the mechanism controlling its uptake will be necessary to project future levels of atmospheric CO_2. Recent work examining CO_2 latitudinal gradients and carbon isotope data has suggested that terrestrial systems are currently a substantial sink for carbon (Tans et al. 1990, Ciais et al. 1995, Francey et al. 1995.) Some authors have suggested that fertilization derived from increased levels of CO_2 (Bacastow and Keeling 1973, Gates 1985, Kohlmaier et al. 1989) might contribute to increasing the size of the terrestrial carbon sink. Kohlmaier et al. (1989) and Hudson et al. (1994) have also suggested that anthropogenic nitrogen emissions might produce a fertilization effect on net carbon sequestration for the terrestrial biosphere.

The second problem is important in that man depends on the productivity of the biosphere for food and fiber. If climate is predicted to change, either with a change in temperature or precipitation or both, then any subsequent change in net primary production could have important consequences for human populations.

Furthermore, any change in the global carbon cycle could produce changes in the atmospheric CO_2 level. For example, Oechel et al. (1993) has suggested that warming, and thereby drying, high latitude soils (Arctic, boreal or high-latitude bogs) could result in increased decomposition and respiration rates resulting in a release of CO_2 to the

atmosphere. McGuire et al. (1992, 1993), Melillo et al. (1993), and Peterjohn et al. (1994) have suggested that increased temperature could accelerate soil decomposition and nitrogen mineralization thereby increasing nitrogen availability and net primary production. Several modeling studies have raised the issue of changes in ecosystem productivity or in the net release or uptake of CO_2 by terrestrial systems using local models (Bonan et al. 1990, Kauppi and Posch 1985, Pittock and Nix 1986) or empirical global models (Smith et al. 1992, Smith and Shugart 1993).

A compelling view of the vegetation, soil, oceans, and atmosphere of the Earth is that of a complex, interacting system in which one treats atmosphere, terrestrial biosphere, and oceans as interacting systems with internal dynamics (Earth System Sciences Committee [ESSC] 1988). This view has been a natural one for studying biogeochemical cycling because of the exchange of elements that occur between media during cycling. Recently, proposals have been advanced for extending this notion to the physical dynamics of the Earth System as well as the biogeochemical dynamics (Ojima 1992). A scheme for a general climate system model has been suggested incorporating atmosphere general circulation model (AGCM); atmospheric chemistry and transport model; terrestrial productivity, cycling, and water process model; ocean general circulation model; and ocean biochemistry model (Dannevik et al. 1994). The goal of constructing such a model would be to have a complete description of the Earth's climate system such that either short term perturbations (e.g., volcanic eruptions) or long term chronic changes (e.g., greenhouse warming) could be studied. In particular, projecting future greenhouse warming due to anthropogenic emissions of CO_2 requires the ability to project future levels of atmospheric CO_2 under various emission scenarios.

To construct a global Earth System model, we are led naturally to a geographically distributed model, i.e., a geographic grid-based model, of the Earth's terrestrial biosphere. This is because a geographically distributed terrestrial model would be a natural structure for coupling the terrestrial model to a AGCM, an atmospheric transport model, or a surface hydrology-surface flow model transporting water and other material to the oceans. In fact we have used the terrestrial model to drive an atmospheric transport model. In this case, we have predicted the seasonal fluctuations of atmospheric CO_2 level (Dignon et al 1994). Even if one rejects the notion of coupling all the models making up the Earth system, geographically distributed terrestrial biosphere models would be useful in assessing the effects of future climates for which it has been predicted that, under rising CO_2 scenarios, the temperature and precipitation changes will occur unevenly over the Earth's surface. For example, the greatest changes in temperature are expected to occur in the winter at high latitudes (Schlesinger and Mitchell 1987). A geographically distributed model of ecosystem processes that are nonlinear in temperature or soil moisture would produce more realistic responses to spatially varying predictions from AGCMs than would simpler, spatially aggregated alternatives.

The first previous work to model the productivity of the terrestrial biosphere on a geographically distributed basis making use of ecosystem response to local climatological variables was based on regression, steady state models of local productivity. Lieth and Box (1972) developed a model of terrestrial primary productivity based on estimated evapotranspiration of Geiger (1965). Leith (1973) suggested the Miami model, which calculates productivity as a function of temperature and precipitation. Leith (1975) described a model of productivity based on the length of the growing season. Meentemeyer et al. (1982) developed a model of terrestrial litter production based on several climatic variables and their combination. These models were designed to produce annual net values and were based on very many, relatively high quality measurements of productivity scattered over the globe. They did not attempt to describe the seasonality of gas exchange.

More recently, geographically distributed models have been designed to follow the dynamics of the elemental pools and fluxes. These models usually incorporate mathematical descriptions of the processes that control the behavior of these systems.

4

Esser (1987, 1991) developed a model to follow carbon dynamics (OBM) for the terrestrial biosphere on a 2.5° grid. In keeping with the terminology introduced by Dannevik et al (1994), we refer to the local site ecosystem submodel that is used in a globally-gridded model as the *kernel* of the global model. Net primary productivity for the kernel of OBM is based on the Miami model modified by a soil productivity factor and a factor for CO_2 level. Potter et al. (1993) developed a model of net primary production and soil decomposition (CASA) for which the net primary productivity of the kernel is driven by the Normalized Difference Vegetation Index (derived from AVHRR satellite data), solar radiation, temperature, and soil moisture. CASA and OBM do not calculate gross primary productivity or plant respiration. Since these two variables respond differently to light, temperature, and soil nutrients that might vary during the year, these models are difficult to adapt to our purposes of calculating gas exchange with the intent of driving an atmospheric transport model. Foley (1994) has developed a model (DEMETER) of biosphere dynamics for which the kernel includes net primary productivity and soil and litter dynamics and is run on a 1° by 1° grid cell. In DEMETER, net primary productivity is separated into gross primary productivity and plant respiration with different dependencies on light and temperature. Carbon processes are not coupled to soil fertility and nitrogen dynamics. Raich et al. (1991), McGuire et al. (1992), McGuire et al. (1993), and Melillo et al. (1993) have developed a model of the coupled carbon and nitrogen dynamics of the terrestrial biosphere (TEM). This model is designed to be coupled to a global hydrological model (WBM) developed by Vorosmarty et al. (1989) which calculates soils moisture content and evapotranspiration using the Thornthwaite method (Thornthwaite and Mather 1957).

There is a vast array of local ecosystem productivity, biogeochemical, or crop-soil system models (e.g., Agren et al. 1991, King and DeAngelis 1985, 1986, 1987, Ng and Loomis 1984, Parton et al. 1987, Running and Coughlan 1988, Running and Hunt 1993, Weinstein et al 1991) that can be used for the kernel of a global ecosystem model. One problem of "globalizing" these models is estimating the parameters for the different ecosystem types or biomes distributed over the globe. A second problem is that more detailed models tend to require more execution time which can become prohibitive at the fine scale of resolution that we would like to achieve. An attractive feature of the kernel of TEM (and the other global models described above) is that it is conceptualized as one model that can be adapted to all ecosystems or vegetation types by properly selected parameters. It is a relatively simple model with relatively few parameters that are reevaluated for each vegetation type.

We have developed a geographically-distributed ecosystem model for the carbon, nitrogen, and water dynamics of the terrestrial biosphere TERRA. In this paper, we describe the basic construction, response to climate change, sensitivity to parameter variation, and self-consistency of the local ecosystem model for carbon, nitrogen, and water of TERRA.

METHODS AND PROCEDURES

Description of TERRA

TERRA consists of coupled modified versions of TEM (Raich et al. 1991) and DAYTRANS (Running 1984). Our overall approach is to build on previous work that suits our criteria for coupling to other components of the Earth's biogeochemical cycles. TEM was selected because it is relatively simple with relatively few parameters yet captures the basic processes of terrestrial productivity and biogeochemical cycling; includes a rudimentary coupling scheme for carbon and nitrogen; responds to soil water content; and separates gross primary production, net primary production, plant respiration, and soil respiration. This latter characteristic of TEM is important in developing seasonal estimates of CO_2 fluxes into and out of the Earth's land surface. For the water balance portion of the computation, we selected DAYTRANS rather than a Thornthwaite-based approach because

DAYTRANS captures more of what is known about transpiration and soil water dynamics.
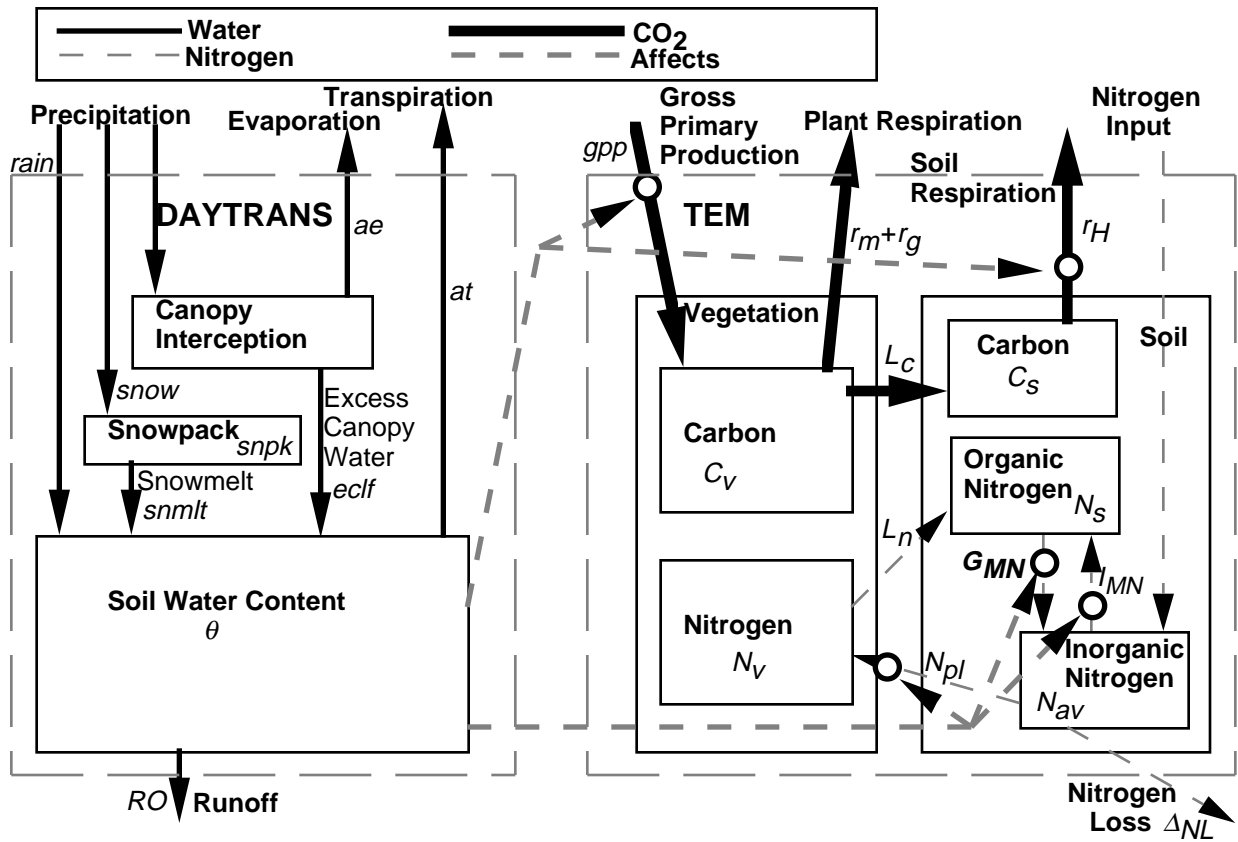
Fig. 1. Schematic diagram of the TERRA model of terrestrial productivity, biogeochemical cycling, and water budget. The figure shows the coupling between the soil water content variable from DAYTRANS and the fluxes in TEM that are in part controlled by soil water.

DAYTRANS is potentially sensitive to other environmental variables such as dew point, solar radiation, daily temperature extremes, etc., unlike the Thornthwaite approach which is determined solely by monthly average temperature and precipitation. By coupling TEM and DAYTRANS within the same framework we are able to allow for future development of dynamic feedback between the two. Fig. 1 shows schematically the structure of coupling DAYTRANS and TEM into one model. Because DAYTRANS and TEM are published elsewhere, we will not describe their functioning in detail. Instead we summarize the models by gathering all equations used in the models into Table A.1 in the appendix. We will concentrate on describing the coupling between TEM and DAYTRANS and the areas in which our implementation differs from the original models. Note that Table 1 contains a glossary of the state variables, intermediate variables, fluxes, parameters dependent on vegetation type, derived parameters, driving variables, calibrated parameters, parameters dependent on soil type, and calibration fluxes. Table 2 is a glossary of universal parameters and constants. Tables 1 and 2 contain entries that reference the equation in Table A.1 in which the parameter or variable is used. This enables one to quickly look up the equation to ascertain the function of the parameter in the model.

The kernel ecosystem model in each grid cell calculates water fluxes of evaporation, transpiration, and runoff; carbon fluxes of gross primary productivity, litterfall, and plant and soil respiration; and nitrogen fluxes of vegetation uptake, litterfall, mineralization, immobilization, and system loss. The state variables are soil water content, carbon in live

Table 1. Description of parameters dependent on vegetation and soil types, variables, and fluxes. Variable lists are for state variables and interim derived variables. The equations that contain the variables and parameters are referenced. The Units column is left blank for unitless parameters.

Symbol	Description	Equation	Units
	State Variables		
ac	Allocation variable regulating CO_2 uptake and nitrogen uptake	A.99, A.74 A.88	
C_s	Carbon content of soil	A.86, A.89 A.82	gC m^{-2}
C_v	Carbon in live vegetation	A.85, A.78 A.94, A.99	gC m^{-2}
$lai(mo)$	Leaf area index	A.83, A.40 A.41, A.42 A.56	
N_{av}	Inorganic soil nitrogen	A.90, A.98 A.95, A.88	gN m^{-2}
N_s	Soil organic nitrogen	A.97, A.89	gN m^{-2}
N_v	Nitrogen in live vegetation	A.94, A.99 A.96	gN m^{-2}
$snpk(jd)$	Snowpack on day jd	A.68	m
$\Theta(jd)$	Soil water content	A.79, A.69	m
$W_{evp}(jd)$	Cumulative evaporation from the canopy	A.72	m
$W_{RO}(jd)$	Cumulative runoff on day jd	A.70	m
$W_{trn}(jd)$	Cumulative transpiration on day jd	A.71	m
	Interim Variables and Fluxes		
$ae(jd)$	Actual evaporation from canopy interception	A.48, A.72	m d^{-1}
$aet_T(mo)$	Actual evapotranspiration as calculated by the Thornthwaite method by WBM.	A.29, A.11	m
aet_{Tmax}	Maximum($aet_T(1)$,..,$aet_T(12)$)	A.11	m
ahd	Absolute humidity deficit	A.38, A.54	g m^{-3}
$at(jd)$	Actual transpiration for the day jd	A.64, A.67 A.73	m d^{-1}
a_{TW}	Thornthwaite exponent for potential evapotranspiration	A.16, A.17	
B	Derived exponent for effect of soil moisture on decomposition	A.80, A.81	
cd	Canopy conductivity	A.51, A.64	s m^{-1}
C_i	Internal leaf CO_2 concentration	A.73, A.74	ppmv
$cn_{hm}(ahd)$	Canopy conductance dependence on absolute humidity deficit	A.54, A.51	
$cn_{lt}(R_{avc})$	Canopy conductance dependence on light	A.55, A.51	
$cn_{slw}(\Psi_s)$	Canopy conductivity dependence on soil water potential	A.52, A.51	s m^{-1}
$cn_{tp}(T_m,T_d)$	Canopy conductivity dependence on daily minimum temperature and average daytime temperature	A.53, A.51	s m^{-1}
$crad$	Average daily radiation absorbed per second	A.59, A.56	J m^{-2} s^{-1}
D	Mean decay state of the active litter as the mean ratio of remaining carbon to initial carbon for most recent six annual cohorts of litter	A.39, A.59 A.63, A.64	

8

Table 1. (Continued)

Symbol	Description	Equation	Units
dayl	Daylength	A.39, A.59 A.63, A.64	s
δ	Solar declination	A.1, A.2	°
Δ_{NL}	Loss of nitrogen from soil	A.95, A.98	gN m^{-2}yr^{-1}
$\Delta_{snD}(id)$	Change in snowpack for the day	A.66, A.68	m d^{-1}
$\Delta_{swD}(id)$	Change in soil water content for the day	A.67, A.69	m d^{-1}
$\Delta_{swT}(mo)$	Change in soil water content in Thornthwaite model	A.27, A.28	m
e_v	Vapor pressure	A.36, A.37	kPa
eclf	Excess canopy interception delivered to soil	A.47, A.67	m d^{-1}
e_s	Saturation vapor pressure at daytime temperature	A.35, A.37	kPa
$f_T(T)$	Response of *gpp* to temperature	A.75, A.74	
γ	Psychrometer constant	A.62, A.56	kPa °C^{-1}
G_{MN}	Gross mineralization of soil nitrogen	A.89, A.93	gN m^{-2} yr^{-1}
gpp	Instantaneous gross primary productivity	A.74, A.83 A.85, A.77	gC m^{-2} yr^{-1}
$H(x)$	Heaviside function	A.7, A.6	
heati	Thornthwaite heat index	A.15, A.16	
I_{MN}	Immobilization of nitrogen by soil bacteria	A.90, A.93	gN m^{-2}yr^{-1}
jdtot(mo)	Number of days in month *mo*	A.24	d
$k_{leaf}(mo)$	Fraction of maximum leaf area index (*lai*) for month mo	A.11-A.14, A.33, A.74	
kleaf$_{max}$	Max($k_{leaf}(1)$,..,$k_{leaf}(12)$)	A.14	
k_{lit}	Bulk annual decay rate of carbon in litter undergoing decomposition and immobilization	A.91, A.92	
K_s	Relative nitrogen diffusion rate	A.87, A.88 A.90	
L_c	Carbon transfer from vegetation to soil by litterfall	A.78, A.85 A.86, A.94	gC m^{-2}yr^{-1}
L_n	Nitrogen transfer from vegetation to soil due to litterfall	A.94, A.97 A.96	gN m^{-2} yr^{-1}
m	Optical air mass	A.3, A.4	
M	Soil water content as percent of saturation	A.79, A.80 A.87	%
moist	Effect of soil moisture on decomposition	A.81, A.82 A.91	
nep	Instantaneous net ecosystem production	A.84	gC m^{-2} yr^{-1}
Nmin	Net mineralization of nitrogen in soil	A.93, A.97 A.98	gN m^{-2}yr^{-1}
N_{pl}	Uptake of nitrogen by vegetation	A.88, A.96 A.98	gN m^{-2}yr^{-1}
npp	Instantaneous net primary production	A.83	gC m^{-2}yr^{-1}
PAR	Daily photosynthetically active radiation	A.9, A.74	J m^{-2}d^{-1}
pe(jd)	Possible evaporation from intercepted precipitation in canopy	A.45, A.47 A.48	m d^{-1}
penmon	Penman-Monteith equation for transpiration	A.56, A.63 A.64	m s^{-1}
pet$_T$(mo)	Thornthwaite estimate of potential evapotranspiration for month *mo*	A.17, A.27 A.29	m
$\phi(\eta)$	Solar altitude	A.2-A.6	radians

Table 1. (Continued)

Symbol	Description	Equation	Units
pre	Limit of evaporation from canopy from radiation	A.46, A.47 A.48	m d^{-1}
Ψ_s	Soil water potential corrected for cold soil	A.50, A.52	kPa
Ψ'_s	Soil water potential uncorrected for cold soil	A.49, A.50	kPa
$pt(jd)$	Potential transpiration for the day jd	A.63, A.73	m d^{-1}
$rain(jd)$	Rainfall for day jd	A.42, A.45 A.65, A.67	m d^{-1}
$rain_T(mo)$	Rainfall rate for month mo	A.22, A.27 A.29	m mo^{-1}
R_{avc}	Average radiation in the canopy per day	A.41, A.55	J m^{-2}d^{-1}
R_{dcan}	Radiation absorbed by the canopy	A.40, A.41 A.56, A.63 A.64	J m^{-2} d^{-1}
r_g	Instantaneous growth respiration	A.77, A.83 A.85	gC m^{-2} yr^{-1}
$r_H(T)$	Respiration from soil decomposition	A.82, A.84 A.86	gC m^{-2} yr^{-1}
ρ_a	Density of dry air	A.60, A.56	kg m^{-3}
$r_m(T)$	Instantaneous maintenance respiration	A.76, A.77 A.83, A.85	gC m^{-2} yr^{-1}
R_n	Net daily shortwave radiation at the Earth's surface	A.8, A.40	J m^{-2} d^{-1}
$RO(id)$	Runoff for the day	A.65, A.67 A.70	m d^{-1}
r_s	Resistance to diffusion of water vapor through leaf stomates	A.57, A.56	s m^{-1}
S_b	Solar beam radiation	A.4-A.6	W m^{-2}
S_d	Diffuse radiation	A.5, A.6	W m^{-2}
$slp(T)$	Slope of saturation vapor pressure curve with respect to temperature	A.58, A.56	kPa $^\circ$C^{-1}
$snmlt$	Potential snowmelt	A.23, A.44	m d^{-1}
$snmlt_D(jd)$	Realized snowmelt for day jd	A.44, A.66	m d^{-1}
$snmt_T(mo)$	Monthly snowmelt rate for Thornthwaite water balance model	A.24, A.25	m mo^{-1}
$snow(jd)$	Snowfall for day jd	A.43, A.66	m d^{-1}
$snow_T(mo)$	Snowfall rate for month mo	A.21, A.25	m mo^{-1}
$snpk_T(mo)$	Snow pack in Thornthwaite water balance model	A.25, A.24	m
ssn	Season of the year	A.8	
S_T	Total solar daily radiation	A.6, A.8	J m^{-2} d^{-1}
$T_{day}(mo)$	Average daytime temperature for month mo	A.19, A.20 A.23, A.35 A.38, A.56 A.60-A.64	$^\circ$C
$\Theta_T(mo)$	Soil water content in Thornthwaite model	A.28, A.27	m
$T_{nt}(mo)$	Average night time temperature for month mo	A.20, A.42 A.43	$^\circ$C
$tsoil$	Temperature of soil	A.34, A.50	$^\circ$C
vpd	Vapor pressure deficit	A.37, A.56 A.63, A.64	kPa
$xlat$	Latent heat of vaporization of water	A.61, A.56	J kg^{-1}

Table 1. (Continued)

Symbol	Description	Equation	Units
	Model parameters depending on vegetation type		
$ahd_t(v)$	Absolute humidity deficit for nominal conductivity	A.54	$g\ m^{-3}$
$al(v,ssn)$	Albedo for vegetation type v and season ssn	A.8	
$a_{leaf}(v)$	Parameter expressing effect of transpiration on lai	A.11	
$b_{leaf}(v)$	Parameter expressing effect of previous monthly value of lai on current month's value	A.11	
$c_{ip}(v)$	Coefficient of canopy interception of precipitation	A.42	$m\ d^{-1}$
$c_{leaf}(v)$	Fraction of leaf area index at minimal levels of transpiration and minimal previous lai	A.11	
$cn_{max}(v)$	Parameter for maximum canopy conductivity	A.52	$s\ m^{-1}$
$ir(v)$	Root type for vegetation type v	A.18, A.30	
$k_{can}(v)$	Absorption coefficient for radiation in the canopy	A.40, A.41	
$lai_{max}(v)$	Maximum leaf area index for vegetation type v	A.33	
$min_{leaf}(v)$	Minimum value of fraction of maximum lai for vegetation type v	A.13	
$p_l(v)$	Correction for projected leaf area for conifers	A.40, A.41	
$r_a(v)$	Air resistance to diffusion of water vapor (leaf boundary layer, canopy turbulent diffusion, boundary layer resistance)	A.56	$s\ m^{-1}$
$s_{ahd}(v)$	Fractional change in conductivity per change in absolute humidity deficit	A.54	$g^{-1}\ m^3$
$T_{max}(v)$	Maximum threshold of response of gpp to temperature	A.75	˚C
$T_{min}(v)$	Minimum threshold of response of gpp to temperature	A.75	˚C
$T_{opt}(v)$	Optimum temperature for response of gpp to temperature	A.75	˚C
$V_{cn}(v)$	Mean annual ratio of carbon to nitrogen in vegetation	A.94, A.99	$gC\ gN^{-1}$
	Derived parameters		
a_{slw}	Coefficient of decay of soil water content under dry conditions	A.26, A.27	$mo\ m^{-1}$
Θ_{fc}	Soil water content at field capacity	A.18, A.31 A.32, A.26	m
Θ_{wp}	Soil water content at wilting point	A.30-A.32	m
w_{co}	Coefficient to convert soil water content to soil water potential	A.31, A.49	
w_{ex}	Exponent to convert soil water content to soil water potential	A.32, A.49	
	Driving variables		
C_a	Atmospheric CO_2 concentration	A.73	ppmv
$dewpt(mo)$	Dew point	A.36	˚C
η	Time of day	A.6, A.2	hr
jd	Julian day of the year	A.63-A.73 A.42-A.45	d
mo	Month of year	A.27-A.29	mo

μ Latitude in degrees   A.2   °

Table 1. (Continued)

Symbol	Description	Equation	Units
$N_{input}(v)$	Instantaneous input of nitrogen to ecosystem from atmospheric deposition and nitrogen fixation	A.98	gN m^{-2} yr^{-1}
$nrd(mo)$	Number of rainy days in month mo	A.42, A.43 A.45	d mo^{-1}
$p(mo)$	Precipitation for month mo	A.42, A.43 A.45	m mo^{-1}
s	Soil texture class	A.18, A.30	
$sh(mo)$	Ratio of actual hours of sunshine to possible sunny hours in month mo	A.8	
$T(mo)$	Average temperature for month mo	A.88, A.82 A.76, A.19 A.91	˚C
$T_{dmax}(mo)$	Average daily maximum temperature for month mo	A.19	˚C
$T_{dmin}(mo)$	Average daily minimum temperature for month mo	A.20	˚C
v	Vegetation type	A.8, A.11 A.52-A.54 A.75, A.76 A.78, A.94 A.95	
External parameters depending on soil type			
$fc_{sat}(s)$	Soil moisture content at field capacity as a percent of saturation	A.87	%
$fc_{sv}(s)$	Soil moisture content at field capacity as a fraction of soil volume	A.18	
$ml(s)$	Power of soil water used to calculate B	A.80	
$m_{opt}(s)$	Optimum soil moisture for maximum decomposition	A.80	
$msat(s)$	Relative decomposition rate above minimum decomposition at fully saturated soil water	A.81	
$pv_{sv}(s)$	Pore volume as a fraction of soil volume for soil texture s	A.79	
$rt(s,ir(v))$	Root depth for soil type s and root type $ir(v)$	A.18, A.30 A.79	m
$wp_{sv}(s)$	Soil moisture content at the wilting point as a fraction of soil volume.	A.30	
Calibrated parameters			
$C_{max}(v)$	Maximum gpp for saturated PAR, saturated C_i, optimal temperature, maximum lai, and maximum ac	A.74	gCm^{-2}yr^{-1}
$K_d(v)$	Decomposition rate per gC m^{-2} of soil carbon at optimal soil moisture and at 0˚C.	A.82, A.91	yr^{-1}
$K_{fall}(v)$	Litterfall transfer per gC m^{-2} of vegetation	A.78	yr^{-1}
$K_r(v)$	Specific maintenance respiration (gC per gC) at 0 ˚C	A.76	yr^{-1}
$L_{nc}(v)$	Ratio of nitrogen to carbon in litterfall	A.94	gN gC^{-1}
$N_{loss}(v)$	Specific rate of loss of nitrogen from soil	A.95	yr^{-1}
$N_{max}(v)$	Uptake rate of nitrogen by vegetation for saturated inorganic soil nitrogen and maximum allocation to nitrogen uptake at 0˚C	A.88	gN m^{-2}yr^{-1}

$N_{up}(v)$ Coefficient of nitrogen immobilization   A.90   gN gC^{-1}

$N_{up}(v)$ Coefficient of nitrogen immobilization   A.90   gN gC^{-1}

Table 1. (Continued)

Symbol	Description	Equation	Units
	Calibration fluxes		
GPP(v)	Gross primary productivity annual flux for vegetation type v	3	gC m^{-2} yr^{-1}
NINPUT(v)	Cumulative annual input of nitrogen to ecosystem for calibration	10	gN m^{-2} yr^{-1}
NPP(v)	Net primary productivity annual flux	5, 6	gC m^{-2} yr^{-1}
NUPTAKE(v)	Annual nitrogen uptake by vegetation used for calibration	7, 8, 9	gN m^{-2} yr^{-1}
RESPAUTO(v)	Total annual respiration flux for vegetation type v equal to GPP less NPP	4	gC m^{-2} yr^{-1}

vegetation, carbon in soil, nitrogen in live vegetation, organic nitrogen in soil and litter, and available inorganic nitrogen aggregating nitrites, nitrates, and ammonia. TERRA follows TEM in that the carbon and nitrogen dynamics are calibrated to specific sites in the 17 vegetation types recognized by TERRA. Calibration fixes eight parameters to reproduce observed fluxes. That is, each calibration parameter is associated with a particular flux.

The global version of TERRA runs on a $1° \times 1°$ grid on the terrestrial biosphere, calculates all fluxes and state variables shown in Fig. 1, and communicates those results to external files. For potential vegetation calculations, we use the data set of Matthews (1983) to fix the vegetation type within each grid cell. TERRA can be coupled to other models of the Earth system such as atmospheric transport models. In this paper we will only discuss the kernel of TERRA.

The seven fundamental equations of the model are the two equations governing carbon conservation in vegetation and soil, eq. A.85 and A.86, respectively; the three equations governing nitrogen conservation in vegetation, the organic soil nitrogen compartment, and the inorganic soil nitrogen compartment, eqs. A.96, A.97, and A.98, respectively; the equation governing the conservation of soil water and the calculation of the new soil water content, eq. A.69; and the equation governing the time development of the state variable *ac* that controls the allocation of resources between carbon uptake and nitrogen uptake, eq. A.99. All other 92 equations of the model (Appendix, Table A.1) are used to construct the terms that are contained in these seven. The terms in these equations contain the ecology, biology, physics, and chemistry that control the dynamics of carbon, nitrogen, and water. For example, gross primary productivity *gpp*, as shown in eq. A.74, is determined by photosynthetically active radiation PAR, internal leaf CO_2, temperature, leaf area index, and the allocation variable.

Coupling DAYTRANS and TEM

As shown in Fig. 1, the soil water content calculated by DAYTRANS affects five fluxes in the TEM submodel. Gross primary production depends on internal leaf CO_2 (eq. A.74) which in turn is determined from the ratio of actual transpiration and potential transpiration (eq. A.63). This ratio depends mainly on the ratio of leaf conductance to maximum leaf conductance. Leaf conductance depends on soil water potential (eq. A.51) which depends on soil moisture content (eq. A.49). This sequence of equations produces the effect that as the soil dries out, soil water potential decreases, leaf conductance decreases, transpiration decreases, and gross primary productivity decreases.

Soil respiration depends on soil moisture through eqs. A.79 through A.82. These functions give the effect of water content on microbial activity and, hence, decomposition and respiration. They produce a response of soil respiration to soil water content that has

Table 2. Synopsis of universal parameters and constants used in the model. The equation that contains the parameter is noted. The Units column is left blank for unitless parameters.

Symbol	Description	Equation	Nominal Value	Units
$adapt$	Maximum rate of change of ac	A.99	0.012[a]	yr^{-1}
α	Scattered radiation contribution to diffuse radiation	A.5	0.5[b]	
β	Absorption of solar beam by gases and aerosols	A.5	0.91[b]	
c_1	Fraction of net radiation below cloudcover for no sunshine hours	A.8	0.33[c]	
c_2	Fraction of net radiation below cloud cover per fraction of sunshine hours of possible sunshine hours	A.8	0.67[c]	
c_{if}	Internal leaf CO_2 concentration as a fraction of external CO_2 level at zero stomatal conductance	A.73	0.1[a]	
cld_1	Fraction of sunlight in photosynthetically active region for cloudy skies	A.9	0.65[a]	
cld_2	Fraction of sunlight in photosynthetically active region for sunny skies	A.9	0.45[a]	
$cldsoil$	Factor increasing the effective soil potential under cold soil conditions	A.50	2.0[d]	
c_p	Specific heat of air at constant pressure	A.56	1010[e]	$J\ kg^{-1}\ °C^{-1}$
d_{cE}	Declination of the Earth	A.1	23.4[b]	°
k_{CO2}	Value of internal CO_2 for response of gpp to be at half maximum	A.74	204[h]	ppmv
k_{lgt}	Value of PAR for response of gpp to be at half maximum	A.74	3.14×10^6[a]	$J\ m^{-2}\ d^{-1}$
k_{n1}	Value of $K_s\ N_{av}$ at which N_{pl} is at half maximum	A.88	1.0[a]	$gN\ m^{-2}$
k_{n2}	Value of $K_s\ N_{av}$ at which I_{MN} is at half maximum	A.90	1.0[a]	$gN\ m^{-2}$
K_{min}	Minimum relative nitrogen diffusion rate at no soil moisture	A.87	0.1[a]	
mst_{mn}	Relative decomposition rate at zero soil water content as fraction of maximum	A.81	0.2[a]	
Ψ_f	Soil water potential at field capacity	A.52, A.31 A.32	-30[f]	kPa
Ψ_w	Soil water potential at the wilting point	A.52, A.31 A.32	-1500[f]	kPa
Q_{10}	Factor increase in maintenance and soil respiration for a 10 °C increase in temperature	A.76, A.82 A.88, A.91	2.0[a]	
r_{grfc}	Fraction of ($gpp - r_m$) used for growth respiration	A.77	0.2[a]	
$sncft$	Snowmelt per degree Celsius	A.23	0.0007[d]	$m\ d^{-1}\ °C^{-1}$
S_p	Solar constant	A.4, A.5	1360[b]	$W\ m^{-2}$
τ	Atmospheric transmission coefficient	A.4	0.7[b]	

Table 2. (Continued)

Symbol	Description	Equation	Value	Units
	Parameters nominally dependent on vegetation type			
$k_{lsr}(v)$	Ratio of the decay rate for litter to that of the whole litter-soil complex	A.91	12.0[g]	
$R_{thr}(v)$	Threshold of radiation for reduction of conductivity	A.55	3×10^6[d]	$J\ m^{-2}d^{-1}$
$s_{nt}(v)$	Change in conductivity per change in night minimum temperature	A.53	0.0002[d]	$m\ s^{-1}\ {}^{\circ}C^{-1}$
$s_{td}(v)$	Fractional change in conductivity per change in average daytime temperature	A.53	0.00003[d]	${}^{\circ}C^{-1}$
$T_{tcd}(v)$	Daytime temperature for nominal conductivity	A.53	10.0[d]	${}^{\circ}C$

[a]Raich et al. 1991; [b]Turton 1986, [c]Jensen et al. 1990, [d]Running 1984, [e]Monteith and Unsworth 1990, [f]Vorosmarty et al. 1989, [g]DeAngelis et al. 1981, [h]Kohlmaier et al. 1989.

an optimum value of soil moisture. For soil moisture either above or below this optimum, respiration falls off.

Soil water mediates the uptake of nitrogen by vegetation through the effect that soil water has on nitrogen diffusion to the root (eq. A.87). This equation produces a strong increase in diffusion rates for an increase in soil moisture. Note the cubic exponent.

Gross mineralization of nitrogen depends on soil respiration. Immobilization of nitrogen depends both on soil respiration and nitrogen diffusion. Both of these variables are functions of soil water content as noted above.

Comparison of TERRA and TEM

Connection of leaf area index computation to water relations –As stated above, TEM is designed to connect to WBM for water relations where TERRA uses DAYTRANS. The one exception to TERRA's use of DAYTRANS is in the calculation of $k_{leaf}(i)$, which is the fraction of the maximum leaf area index that is currently attained for a particular cell for month i. For the calculation of k_{leaf}, TERRA uses a WBM-type Thornthwaite calculation rather than the Penman-based DAYTRANS. The calculation of k_{leaf} is given in eqs. A.10 through A.29. Note that the basic equation for k_{leaf}, eq. A.11, contains three coefficients a_{leaf}, b_{leaf}, and c_{leaf}. These three coefficients were originally determined by McGuire et al. (1992) by regression of each month's leaf area index to the two independent variables: the previous month's leaf area index and $aet_T(i)/aet_{Tmax}$ the ratio of actual evapotranspiration to maximum attained evapotranspiration for the cell. The latter values were determined from the Thornthwaite calculations of WBM. So we have assumed that eq. A.11 needs to be implemented using a WBM-type calculation for $aet_T(i)$ and aet_{Tmax}. Therefore eqs. A.15 through A.29 are our implementation of WBM using the Thornthwaite method.

Water relations and gross primary productivity.–Raich et al. (1991) uses actual evapotranspiration and potential evapotranspiration (as calculated by WBM) instead of actual transpiration and potential transpiration (as calculated by DAYTRANS that TERRA uses) in the their equation analogous to our eq. A.73. Because TERRA does not use the evaporation terms in this ratio, but TEM does, in calculating internal leaf CO_2, substantial numerical differences can occur between the two approaches in calculating the effect of stomatal action on gross primary production. To see this more clearly, consider the motivation behind the use of the analog to eq. A.73 in TEM for calculating internal leaf

18

CO_2 concentration from external atmospheric CO_2. Assuming a Michaelis-Menten type response of gross photosynthesis to internal CO_2 concentration, if one equates gross photosynthesis less respiration to the net diffusion rate of CO_2 between the reference atmosphere level and the internal leaf as controlled by a series of resistances, one finds that internal CO_2 is approximately proportional to external CO_2. The constant of proportionality is given by the inverse of the total resistance, which is dominated by stomatal conductance. Now the ratio of Penman's equation (eq. A.56) using actual or realized stomatal conductance cd to Penman's equation using maximum stomatal conductance cn_{max} is the ratio of stomatal conductance to maximum stomatal conductance times a very slowly varying function of stomatal conductance that changes very little over the course of a growing season. Thus eq. A.73 is a reasonable model for the relation of C_i to C_a. The architects of TEM were forced to find a surrogate for stomatal conductance because WBM did not calculate leaf conductance but only actual evapotranspiration and potential evapotranspiration. In TERRA, we could have used leaf conductance directly in eq. A.73 instead of at and pt because DAYTRANS calculates leaf conductance cd. However, the ratio that TERRA uses follows the spirit of TEM, is very close to the more rigorous cd/cn_{max}, and is adequate to give realistic results. If we were to have used evapotranspiration (as TEM does) instead of transpiration (as TERRA does) to estimate $cd/cnmax$, we would have a less realistic relation of C_i to C_a. In part, this is because evaporation in natural systems can be up to 50% of total evapotranspiration. Also, in tropical systems potential evaporation can be quite high and actual evaporation will not supply the demand. The use of evapotranspiration in the C_i calculation can lead to unrealistically high levels of C_{max} (parameter for gross primary productivity at optimum conditions) for tropical systems to compensate for the small ratio of actual evapotranspiration to potential evapotranspiration.

Net radiation submodel.–In the calculation of net radiation used in TERRA eq. A.8, we included the albedo for each season for each vegetation type as given by Matthews (1984). Instead of using cloud cover in eq. A.8, we used the fraction of actual sunshine hours to potential sunshine hours to calculate the effect of cloudiness on solar radiation following the method of Doorenbos and Pruitt (1977) as given by Jensen et al. (1990).

Dependence of gross primary productivity on temperature.–We use the same function for dependence of gpp on temperature f_T that Raich et al. (1991) uses. In later versions of TEM, McGuire et al. (1992) replaced f_T with a function that was identical to it for temperatures below the optimum temperature at T_{opt} and was equal to 1 for temperatures above the optimum. Note that f_T is equal to 1 at the optimum temperature T_{opt}. We retain use of the older version because the shape of the mathematical function below the optimum temperature is in part determined by the value of the maximum temperature allowed for gross primary productivity T_{max}.

Immobilization of nitrogen.–Immobilization of nitrogen is dominated by decomposition in the litter (Raich et al. 1991; Waring and Schlesinger 1985; Aber and Melillo 1980, 1982; Melillo and Aber 1984). In deriving D for eqs. A.90 through A.92, Raich et al. (1991) specifically point out that cohorts of litter older than six years old contribute little to the immobilization of nitrogen. Thus the annual decay rate of litter should be used in the exponential giving the decay of litter in the formula for D eq. A.92. Noting that K_d is the decay rate for the whole soil column, we have introduced the factor $k_{lsr}(v)$ such that the product $k_{lsr}(v)K_d$ is the decay rate for the litter layers.

Constants treated as parameters.–We treat c_i, r_{grfc}, mst_{mn}, and K_{min} as parameters in TERRA rather than as constants. The practical effect of this is that in the sensitivity analysis described below these parameters are tested with the rest to determine the sensitivity of the model results to variations in them or their uncertainty.

Allocation submodel.–The nitrogen-carbon coupling that we use in this report is exactly the same as used in the original version of TEM as described by Raich et al. (1991).

19

It is based on the model of Rastetter and Shaver (1992) that simulates allocation of resources among the various uptake pathways for the different nutrients required by the plant. Acclimation by shifting resources to compensate for reduced availability of some nutrients is well known and Rastetter and Shaver (1992) review the mechanisms used to achieve this. The submodel operates by adjusting the variable ac by eq. A.99. If the C:N ratio is too large (i.e., exceeds V_{cn} the nominal, correct balance of carbon and nitrogen required by the plant), then ac is reduced by eq. A.99. For a smaller ac, gross primary productivity (carbon uptake) is decreased (eq. A.74) and nitrogen uptake is increased (eq. A.88). The reverse occurs if the C:N ratio is too small. The rate at which ac adjusts (acclimation occurs) is determined by the parameter *adapt*. We use the same value of 0.012 yr^{-1} as Raich et al. (1991). Thus the relaxation time of acclimation is about 83 years. Raich et al. (1991) chose this value of *adapt* arbitrarily but argued that its value does not affect equilibrium (steady state) results.

We retain this original version of carbon-nitrogen coupling for this report because it is an important approach in the range of mechanisms of nitrogen fertilization and we believe it should be explored. In this approach controlling the C:N ratio to an optimum value is the dominant mechanism for nutrient response. Therefore this approach can be regarded as one end of a plasticity scale of the C:N ratio produced by different mechanisms and gives us one limit on the range of dynamical behavior. Because one of our goals is to understand the dynamics of this formulation in the multi-year transient response, the large acclimation times are an advantage. The time scale for acclimation chosen by Raich et al. (1991) is larger than that for most of the other direct effects on *gpp* and much smaller than that for soil decomposition times. Thus, this value for *adapt* facilitates the analysis because the effects of the different processes are separated in time.

We emphasize that both Raich et al (1991) and McGuire et al (1992) state that the arbitrary size of adapt does not affect the results in the steady state calculations. Furthermore, because of the long time scale for acclimation imposed by the value of *adapt*, this approach does not affect the seasonal results of carbon dynamics after acclimation occurs.

Subsequent versions of TEM (McGuire et al. 1992, McGuire et al. 1993) use substantially different approaches to couple carbon and nitrogen dynamics. We also have developed a different version of TERRA with a more direct carbon-nitrogen coupling which will be discussed elsewhere.

Comparison of TERRA and DAYTRANS

Our implementation of DAYTRANS varied slightly from that published by Running (1984). The refinements or modifications were usually designed to extend the applicability of DAYTRANS beyond its original scope.

Penman equation modifications.–The Penman-Monteith equation as used in the DAYTRANS version of FOREST-BGC (Running and Coughlan 1988) was modified to the form given by Monteith and Unsworth (1990), Thom (1975) and Jensen et al. (1990). The effect of this change is to rationalize the use of the Penman equation over many layers of leaf area index so that the functional dependence of transpiration on leaf area index was brought into agreement with the cited literature, eqs. A.56, A.63, and A.64. Average net radiation in the canopy was changed to net radiation absorbed by the canopy, eq. A.40. We also changed the calculation of vapor pressure deficit so that it is based on dewpoint and average daytime temperature, eqs. A.35 to A.37.

Extrapolation to other vegetation types.–The original DAYTRANS was developed for temperate coniferous forests. We extrapolated DAYTRANS to other vegetation types by first assuming that all parameters of the model were vegetation-type dependent. The parameters treated in this way were maximum leaf area index lai_{max}, coefficient of radiation absorption in the canopy k_{can}, coefficient of precipitation interception by the canopy c_{ip},

maximum stomatal conductance cn_{max}, coefficient for response of conductance to night temperature s_{nt}, coefficient for response of conductance to day temperature s_{td}, threshold of response of conductance to absolute humidity deficit ahd_t, threshold of radiation for stomatal conductance R_{thr}, coefficient of response of conductance to absolute humidity

Table 3. Input parameters associated with vegetation types for the submodels for leaf phenology and carbon dynamics. Units are given in Table 1.

System Number	Vegetation type	$T_{min}^{a,b}$	T_{max}^{b}	$T_{opt}^{a,b}$	a_{leaf}^{a}	b_{leaf}^{a}	c_{leaf}^{a}	min_{leaf}^{a}
1	Polar desert/alpine tundra	-1.0	33	15	0.7964	0.4664	–0.0287	0.00
2	Wet/moist tundra	-1.0	33	15	0.7964	0.4664	–0.0287	0.00
3	Boreal woodland	-1.0	37	15	0.7149	0.2944	0.1329	0.20
4	Boreal forest	-1.0	37	15	0.4289	0.3330	0.3223	0.50
5	Temperate coniferous forest	-1.0	42	18	0.0000	0.0000	0.0000	1.00
6	Arid shrubland	1.0	55	31	0.4640	0.6708	–0.0068	0.25
7	Short grassland	0.0	50	27	0.4437	0.6520	0.0098	0.10
8	Tall grassland	0.0	48[c]	27	0.4746	0.5807	–0.0564	0.05
9	Temperate savanna	-1.0	50	24	0.7808	0.4427	–0.0828	0.05
10	Temperate deciduous forest	-1.0	45	20	0.8330	0.3520	–0.0754	0.02
11	Temperate mixed forest	-1.0	45	19	0.4162	0.3516	0.2874	0.50
12	Temperate broadleaved evergreen forest	0.0	44[c]	25	0.0000	0.0000	0.0000	1.00
13	Mediterranean shrubland	-1.0	49[c]	25	0.2669	0.9592	–0.0773	0.25
14	Tropical savanna	1.0	50[c]	30	0.3366	0.6451	0.0422	0.15
15	Xeromorphic woodland	-1.0	49[c]	25	0.4423	0.5426	0.0713	0.25
16	Tropical deciduous forest	0.0	48[c]	27	0.4423	0.5426	0.0713	0.25
17	Tropical evergreen forest	2.0	48[c]	28	0.4423	0.5426	0.0713	0.25

[a]McGuire et al. 1992, [b]Larcher 1990 except as noted, [c]Raich et al. 1991.

Table 4. Input parameters associated with vegetation types for the submodels for allocation and radiation. Units are given in Table 1.

System Number	Vegetation type	V_{cn}^{a}	$al(v,wi)^{b}$	$al(v,sp)^{b}$	$al(v,su)^{b}$	$al(v,fa)^{b}$
1	Polar desert/alpine tundra	69.2	.12	.12	.17	.15
2	Wet/moist tundra	50.0	.12	.12	.17	.15
3	Boreal woodland	91.7	.14	.14	.16	.14
4	Boreal forest	375.	.11	.12	.15	.12
5	Temperate coniferous forest	580.	.11	.12	.15	.12
6	Arid shrubland	27.7	.28	.32	.28	.28
7	Short grassland	35.8	.16	.2	.2	.18
8	Tall grassland	108.	.17	.17	.2	.17
9	Temperate savanna	131.	.14	.15	.17	.15
10	Temperate deciduous forest	419.	.12	.15	.18	.13
11	Temperate mixed forest	411.	.12	.15	.18	.13
12	Temperate broadleaved evergreen forest	357.	.12	.13	.14	.13
13	Mediterranean shrubland	46.4	.15	.14	.15	.14
14	Tropical savanna	57.3	.14	.15	.17	.15
15	Xeromorphic woodland	46.4	.28	.32	.28	.28
16	Tropical deciduous forest	66.4	.18	.16	.15	.16
17	Tropical evergreen forest	75.5	.11	.11	.11	.11

[a]From Table 9, [b]Matthews 1984.

Table 5. Parameters associated with vegetation types for the water balance submodel DAYTRANS. Units are given in Table 1.

System Number	lai_{max}	c_{ip}^q	p_l	k_{can}	cn_{max}	s_{ahd}	ahd_t	r_a	ir^{zz}
1	0.18[a]	0.0002	1.0	0.9[s]	0.0031[aa]	0.057[oo]	6.6[oo]	104.2	1
2	1.0[b]	0.0002	1.0	0.7[t]	0.0057[bb]	0.058[oo]	6.7[oo]	84.8	1
3	6.0[c]	0.00014[c,z]	2.0[c,r]	0.42[c]	0.0026[c]	0.051[c]	4.2[c]	17.5	1
4	11.[d]	0.00013[z]	2.2[r]	0.55[u]	0.0023[cc]	0.05[pp]	4.0[pp]	22.8	2
5	12.[e]	0.00012[z]	2.2[r]	0.55[u]	0.0027[dd]	0.05[pp]	4.0[pp]	18.2	2
6	0.94[f]	0.0002	1.0	0.9[v]	0.0065[ee]	0.031[qq]	11.2[qq]	44.7	1
7	1.4[g]	0.0002	1.0	0.47[w]	0.0069[ff]	0.03[rr]	3.5[rr]	67.3	1
8	3.1[h]	0.0002	1.0	0.47[w]	0.0081[gg]	0.028[ss]	3.9[ss]	54.9	1
9	3.83[i]	0.0002	1.0	0.44[i]	0.0065[i]	0.035[i]	4.0[i]	44.8	1
10	6.0[j]	0.0002	1.0	0.57[x]	0.0041[hh]	0.045[tt]	4.1[tt]	42.3	2
11	9.0[c]	0.00014[c,z]	1.56[c,r]	0.55[c]	0.0032[c]	0.048[c]	4.0[c]	30.2	2
12	7.7[k]	0.0002	1.0	0.57[x]	0.0039[ii]	0.033[uu]	7.5[uu]	26.9	2
13	2.3[l]	0.0002	1.0	0.9[v]	0.0052[jj]	0.035[vv]	7.5[vv]	65.3	1
14	4.1[m]	0.0002	1.0	0.49[y]	0.0077[kk]	0.038[ww]	4.0[ww]	62.3	1
15	4.3[n]	0.0002	1.0	0.57[x]	0.003[ll]	0.033[xx]	10.2[xx]	60.7	1
16	6.0[o]	0.0002	1.0	0.57[x]	0.0052[mm]	0.047[yy]	5.5[yy]	81.6	2
17	7.3[p]	0.0002	1.0	0.6[z]	0.0045[nn]	0.047[yy]	5.5[yy]	63.0	2

[a]Shaver and Chapin 1991, [b](Shaver and Chapin 1991, Dennis et al. 1978), [c]Based on cover estimates of McGuire et al. 1992, [d]DeAngelis et al. 1981, [e](DeAngelis et al. 1981, Schulze 1982, Jarvis et al. 1976), [f](Caldwell et al 1977, Whittaker and Niering 1975, Smith and Nowak 1990), [g](Sims and Coupland 1979, Ripley and Redmann 1976, Numata 1979), [h](Conant and Risser 1974, Sims and Coupland 1979, Ripley and Redmann 1976, Numata 1979), [i]Based on cover measurements of Ovington et al. 1963, [j](DeAngelis et al. 1981, Schulze 1982, Jarvis and Leverenz 1983, McIntyre et al. 1990, Burton et al. 1991, Wang et al. 1992), [k](Schulze 1982, Jarvis and Leverenz 1983, Miller 1963a, Satoo 1983), [l](Schulze 1982, Kummerow et al. 1981, Miller et al 1981, Mooney 1988, Ehleringer and Mooney 1983), [m](Kinyamario and Imbamba 1992, Medina 1982, Huntley and Morris 1982, Misra 1983, Medina and Klinge 1983), [n]Murphy and Lugo 1986, [o](Ramam 1975, DeAngelis et al. 1981, Schulze 1982, Medina and Klinge 1983), [p](Schulze 1982, Medina and Klinge 1983, Edwards and Grubb 1977, Tanner 1980, Laumonier et al. 1991), [q]Based on Dickinson et al. 1986 except as noted, [r]Based on Running 1984, [s]Lewis and Callaghan 1976, [t](Lewis and Callaghan 1976, Miller et al. 1984), , [u](Running and Coughlan 1988, Jarvis et al. 1976, Jarvis and Leverenz 1983), [v]Miller et al 1981, [w]Ripley and Redmann 1976, [x]Jarvis and Leverenz 1983, [y]Kinyamario and Imbamba 1992, [z]Waring and Schlesinger 1985, [aa](Lewis and Callaghan 1976, Oberbauer and Oechel 1989, Korner et al. 1983) [bb](Lewis and Callaghan 1976, Gates 1980, Miller et al. 1978, Oberbauer and Oechel 1989), [cc](Carter et al. 1988, Goldstein et al. 1985), [dd](DeLucia and Schlesinger 1990, Jarvis et al. 1976, Gates 1980, Watts et al. 1976, Jarvis et al. 1985, Waring and Schlesinger 1985, Waring et al. 1981, Running and Hunt 1993, Leverenz et al. 1982, Graham and Running 1984, Carter et al. 1988, Smith et al. 1984, Schulze and Hall 1982, Day et al. 1989), [ee](Ehleringer and Mooney 1983, DeLucia and Schlesinger 1990, Nilsen et al. 1983, Forseth et al. 1984, Blake-Jacobson 1987, Caldwell et al. 1977, Knapp and Smith 1987, Szarek and Woodhouse 1976, Davis and Mooney 1985, Schulze and Hall 1982), [ff](Smith and Nowak 1990, Ripley and Redman 1976, Dunin et al. 1978, Sala et al. 1982, Ripley and Saugier 1978,

Roy et al. 1987, Running and Hunt 1993, Monson et al. 1986), [gg](Knapp 1985, Barnes 1985, Running and Hunt 1993), [hh](Reich and Hinckley 1989, Turner and Heichel 1977, Smith and Knapp 1990, Federer and Gee 1976, Kozlowski et al. 1991, Allen and Lemon 1976, Gates 1980, Waring and Schlesinger 1985, Waring et al. 1981, Running and Hunt 1993, Jurik 1986, Schulze and Hall 1982), [ii](Sharma 1984, Waring and Schlesinger 1985,De Lillis and Sun 1990, Korner and Cochrane 1985), [jj](Rhizopoulou and Mitrakos 1990, Poole et al. 1981, Blake-Jacobson 1987, Correia et al. 1987, Larcher 1991, Davis and Mooney 1985, Gollan et al. 1985), [kk](Medina 1982, Kinyamario and Imbamba 1992, Meinzer et al. 1983, Korner et al. 1983), [ll](Ulmann et al. 1985, Korner 1994), [mm](Korner 1994, Fetcher 1979), [nn](Dolman et al. 1991, Allen and Lemon 1976, Robichaux et al. 1984, Kapos and Tanner 1985, Aylett 1985, Roberts et al. 1990), [oo]Johnson and Caldwell 1976, [pp]Running 1984, [qq](Nilsen et al. 1983, Schulze and Hall 1982), [rr](Smith and Nowak 1990, Kelliher et al. 1993), [ss](Barnes 1985, Kelliher et al. 1993), [tt](Federer and Gee 1976, Waring and Schlesinger 1985, Osonubi and Davis 1980, Schulze and Kuppers 1979, Running and Hunt 1993), [uu](Waring and Schlesinger 1985, Korner and Cochrane 1985), [vv](Gollan et al. 1985, Turner et al. 1984), [ww]Korner et al. 1983, [xx]Ullman et al. 1985, [yy](Chiariello 1984, Roberts et al. 1990, Osonubi and Davis 1980), [zz]Vorosmarty et al. 1989.

deficit s_{ahd}, coefficient for projected leaf area p_l, and aerodynamic resistance to water vapor exchange between the atmosphere and the leaf r_a. Discussions of parameter estimation are given below.

Extended daylength calculation.–The daylength calculation, eq. A.39, was generalized to be valid for high latitudes in both summer and winter and for the southern hemisphere. It was also converted to the method of Swift et al. (1976).

Generalization of low temperature effect on root resistance.–The effect of soil temperature on root resistance, eq. A.50, was generalized to the cold systems (tundra and boreal). TEM and TERRA do not have a complete description of the propagation of heat into the soil and hence do not calculate permafrost. McGuire et al. (1992) report that this is compensated for in TEM by fixing soil moisture at field capacity in cold systems during TEM simulations. We do not follow that approach. Instead, recognizing that these systems will maintain low soil temperatures, we apply to those systems the DAYTRANS prescription for simulating the increase in root resistance at low temperature, i.e., increasing soil potential.

Use of aerodynamic resistance to gas exchange.–As noted above, we generalize the use of aerodynamic resistance to water vapor exchange between the atmosphere and leaf r_a from temperate coniferous forests by calculating values for each vegetation type. Formulas for its calculation are given in table A.2 in the appendix. We break r_a into three components: resistance from a reference height to the canopy top (Jensen et al. 1990), resistance within the canopy from the canopy top to the average canopy depth (Thom 1975), and boundary layer resistance of the leaf (Gates 1980). Characteristics of the canopies, leaves, and typical wind values for the calibration sites are given in Table A.3. We move these parameters to the appendix and the equations into a separate table in the appendix because the calculated values of r_a were inputs to TERRA, not the aerodynamic characteristics of leaves or canopies nor windspeeds. The treatment of r_a as a parameter and not a function follows the practice in the original DAYTRANS and was rationalized on the basis that aerodynamic resistance is usually small compared to stomatal resistance. A stronger justification for this approach is that the sensitivity analysis reported below demonstrates that changes in r_a have only negligible impacts on carbon and nitrogen dynamics. Thus a more detailed calculation of r_a within TERRA would not produce noticeably different results in carbon and nitrogen behavior.

The model parameters of TERRA are taken from literature sources except for the eight parameters determined from calibration. The calibration procedure is described in the next section. Table 2 shows the universal biological parameters that apply to all vegetation systems (e.g., Q_{10}, c_{if}, etc.) or the physical parameters that are independent of the system (e.g., α, cld_1, cld_2, etc.). The literature sources for all these parameters are given in the table footnotes. Note that all parameters that were treated as universal in TEM were treated as universal in TERRA.

We estimated the new parameter for the ratio of the litter decomposition rate to the soil decomposition rate $k_{lsr}(v)$ using data for all woodland data sets from DeAngelis et al (1981) for which this ratio could be estimated. We used this average value globally for all vegetation types.

Tables 3 through 5 contain the parameters dependent on vegetation type. The parameters T_{min}, T_{max}, and T_{opt} determine the response of *gpp* to temperature. The values of T_{min} and T_{opt} were taken from McGuire et al. (1992) who estimated them from Larcher (1991). The values for T_{max} were extracted from Larcher (1991) either by the authors or by Raich et al. (1991) as noted in Table 3. The parameters a_{leaf}, b_{leaf}, c_{leaf}, and min_{leaf} determine the seasonal development of foliage as a function of evapotranspiration. The values for these parameters were taken from McGuire et al. (1992) The values for V_{cn} are found by taking the ratio of the annual averages of carbon in vegetation C_v to nitrogen in vegetation N_v as given in Table 9. The parameters for albedo $al(v, season)$ are from Matthews (1984). The albedo affects both light in the submodel for carbon assimilation and the evapotranspiration of water in the water balance submodel.

The parameters in Table 5 are used in DAYTRANS. The determination of the values for these parameters was necessary for the globalization of DAYTRANS. The parameter lai_{max} is the maximum leaf area index occurring at the peak of the growing season. The values were taken from the studies at the calibration sites or were averages over communities belonging to the vegetation type. The parameter values for interception of precipitation by the canopy c_{ip} are mainly taken from Dickenson et al. (1986) except for the conifer systems for which c_{ip} was estimated from data in Waring and Schlesinger (1985). The factor for projecting the leaf area index of coniferous systems is taken from Running (1984). The parameter controlling absorption of radiation in the canopy k_{can} was not usually measured in the studies on which calibration is based. Instead we used typical values for each vegetation system as given in the references for Table 5. There is not an extensive data base for maximum stomatal conductivity, response of conductivity to humidity, or the threshold of the onset of the response to humidity. However, there is enough data to make tentative generalizations for each of the 17 vegetation types. (We anticipate that the scientific community will expand this baseline data very rapidly and that future estimates of the dynamics in coupled water-carbon-nitrogen calculations can be improved.) In some systems, these values seem to be reasonably robust; in others, our knowledge is less secure. One source of variation seems to be the different "life strategies" employed by different species in a community. For example, in arid systems some deciduous shrubs have relatively high values for cn_{max} while evergreen shrubs often have much lower values for cn_{max}. The values for aerodynamic resistance to water vapor exchange r_a were calculated using the equations in Table A.3 and data in Table A.4; both tables are in the appendix.

Following the approach of McGuire et al. (1992), the parameters in Table 5 for the vegetation types of boreal woodland, temperate savanna, and temperate mixed forest were estimated by combining the parameters for the constituent subsystems based on the cover weightings given by McGuire et al. (1992) for these three vegetation types. The value of c_{ip} was determined such that the total rainfall intercepted by the system was the same as the

sum of the rainfall intercepted by the constituent systems. Likewise, the parameter for

Table 6. Parameters dependent on soil type. Units are given in Table 1.

Soil Type	Soil Textural Group	$fc_{sat}(s)$[a]	$fc_{sv}(s)$[a]	$ml(s)$[b]	$m_{opt}(s)$[b]	$msat(s)$[b]
1	Coarse - S, LS	39.0	0.141	0.356	59.0	0.5
2	Moderately Coarse - LVFS, SL	48.5	0.2	0.308	64.0	0.5625
3	Medium - VFSL, L, SiL, Si	58.1	0.273	0.14	68.0	0.625
4	Moderately Fine - CL, SCL, SiCL	68.4	0.352	-0.624	71.0	0.6875
5	Fine - SC, SiC, C	88.7	0.485	-1.883	73.0	0.75
6	Lithosol	58.1	0.273	0.14	68.0	0.625

[a]Vorosmarty et al. 1989, [b]Raich et al. 1991.

Table 7. Parameters dependent on soil type. All data is taken from Vorosmarty et al. 1989. Units are given in Table 1.

Soil Type	Soil Textural Group	$rt(s, ir=1)$	$rt(s, ir=2)$	$pv_{sv}(s)$	$wp_{sv}(s)$
1	Coarse - S, LS	1.0	2.5	0.362	0.063
2	Moderately Coarse - LVFS, SL	1.0	2.0	0.412	0.091
3	Medium - VFSL, L, SiL, Si	1.3	2.0	0.47	0.132
4	Moderately Fine - CL, SCL, SiCL	1.0	1.6	0.515	0.2
5	Fine - SC, SiC, C	0.7	1.2	0.547	0.358
6	Lithosol	0.1	0.1	0.47	0.132

radiation extinction in the canopy k_{can} was fixed such that total radiation absorbed by the canopy by the combined system equaled the sum of the radiation absorbed by the constituent systems. The parameters cn_{max}, s_{ahd}, and ahd_t for these three systems were estimated by averaging the parameters of the constituent systems using the product of leaf area index and cover for the relative weights.

Tables 6 and 7 contain all the parameters dependent on the six soil types. The parameters for field capacity as a percent of pore volume fc_{sat}, field capacity as a fraction of soil volume fc_{sv}, and rooting depth rt are all taken from Vorosmarty et al. (1989). The parameters used to calculate the dependence of decomposition on soil water (ml, m_{opt}, and $msat$, eqs. A.80 through A.82) were taken from Raich et al. (1991).

Estimation of k_{CO2}.–The fertilization effect of CO_2 on the terrestrial biosphere has been considered by many authors (e.g., Bacastow and Keeling 1973, Gates 1985, Kohlmaier et al. 1989) who commonly quantify the effect using the variable $\hat{\beta}$

$$\hat{\beta} = \frac{\delta npp}{\delta C_a} \frac{C_a}{npp} \tag{1}$$

Kohlmaier et al. (1989) reviewed the literature of CO_2 exposure experiments and found that $\hat{\beta}$ is best approximated by 0.375±0.225. The value of $\hat{\beta}$=0.375 corresponds to a k_{CO2} equal to 204 ppmv assuming optimal growing conditions (no other limiting factors.) This is the value of k_{CO2} that we use in our calculations.

The aerodynamic resistance parameter is determined for each vegetation type using equations from Jensen et al. (1990) (eqs. A.100-A.102, A.106) to calculate resistance from the reference height to the top of the canopy, Thom (1975) (A.103-A.105, A.107) to calculate resistance from the top of the canopy to the displacement height, and Gates (1980) (A.108) to calculate the leaf boundary layer resistance. The data needed as input for these

equations, windspeed at the reference height $u(H_v+z)$, height of the canopy H_v, and leaf dimensions D_L and W_L are given in Table A.4. Values for D_L and W_L are found by averaging the leaf characteristics over the species listed by the primary work for the calibration site. Leaf characteristics for individual species were taken from flora descriptions. Canopy height was usually taken from the documentation for the calibration site. In some instances it was estimated by averaging over several sites representative of the vegetation type. Total aerodynamic resistance is the sum of the three aerodynamic resistances (eq. A.109). The resulting r_a is given in Table 5.

Calibration of TERRA.

Eight parameters are determined during calibration for each of the 17 vegetation types. These parameters are associated with the eight fluxes of gross primary productivity (C_{max}), plant respiration (K_r), carbon transfer by litterfall (K_{fall}), soil respiration (K_d), nitrogen uptake by vegetation (N_{max}), nitrogen transfer by litterfall (L_{nc}), nitrogen immobilization (N_{up}), and nitrogen loss from the system (N_{loss}). The calibration process satisfies the conditions that (1) the system is in steady state; (2) gross primary production *GPP*, which is the input to the carbon vegetation compartment over one year, is equal to observed net primary production (*NPP*) plus total plant respiration (*RESPAUTO*); (3) total plant respiration equals *RESPAUTO*; (4) total carbon transfer by litterfall equals *NPP*; (5) total soil respiration equals *NPP*; (6) total nitrogen lost by the system equals total input (*NINPUT*); (7) total nitrogen taken up over the year equals *NUPTAKE*; (8) total transfer of nitrogen from plants to soil organic nitrogen by litterfall equals *NUPTAKE*; and (9) net mineralization (gross mineralization less immobilization) equals *NUPTAKE*. The calibration process also is designed to satisfy the condition that the annual averages of the standing crop of carbon in vegetation, carbon in soil, nitrogen in vegetation, organic nitrogen in soil, and inorganic or available nitrogen in soil, denoted by $\langle C_v \rangle$, $\langle C_s \rangle$, $\langle N_v \rangle$, $\langle N_s \rangle$, and $\langle N_{av} \rangle$, respectively, fit measured values as given in Table 9. The definition of the annual time-average of each parameter is the integral over one year. For example,

$$\langle C_v \rangle = \frac{1}{T} \int_0^T C_v \ dt = \int_0^1 C_v \ dt. \tag{2}$$

where the time period T over which the variable is averaged is chosen as one year. Similar equations apply to the other four standing crops. Finding standing crops that satisfy eq. 2 for all state variables is achieved by adjusting the initial values of C_v, C_s, N_v, N_s, and N_{av} at the beginning of each iteration until the time-averaged values of each state variable averaged over the year converge to the observed values. During calibration, the grid cell model is run iteratively by annually varying the eight calibration parameters until steady state is achieved. The definition of convergence or steady state is that the sum of the absolute relative changes over all parameters plus the sum of absolute relative differences between time-averaged standing crops and target values must be less than one part in a million. The iteration equations for the parameters for the $k+1$ iteration are

$$C_{max,k+1} = \frac{GPP}{\dfrac{1}{C_{max,k}} \displaystyle\int_0^1 gpp_k\left(PAR, C_i, T, ac; \{p_{i,k}\}\right) \ dt} \tag{3}$$

29

$$K_{r,k+1} = \frac{RESPAUTO - r_{grf} \int_0^1 \left[gpp_k\left(PAR, C_i, T, ac; \{p_{i,k}\}\right) - r_{m,k}\left(T; \{p_{i,k}\}\right) \right] dt}{\dfrac{1}{K_{r,k}} \int_0^1 r_{m,k}\left(T; \{p_{i,k}\}\right) dt}$$ (4)

$$K_{fall,k+1} = \frac{NPP}{\int_0^1 C_{v,k} \, dt}$$ (5)

$$K_{d,k+1} = \frac{NPP}{\dfrac{1}{K_{d,k}} \int_0^1 r_{H,k}\left(T, \Theta; \{p_{i,k}\}\right) dt}$$ (6)

$$N_{max,k+1} = \frac{NUPTAKE}{\dfrac{1}{N_{max,k}} \int_0^1 N_{pl,k}\left(N_{av,k}, T, ac, \Theta; \{p_{i,k}\}\right) dt}$$ (7)

$$L_{NC,k+1} = \frac{NUPTAKE}{\dfrac{1}{L_{nc,k}} \int_0^1 L_{n,k}\left(\{p_{i,k}\}\right) dt}$$ (8)

$$N_{up,k+1} = \frac{\left(NUPTAKE - \int_0^1 G_{MN,k}\left(T, \Theta; \{p_{i,k}\}\right) dt \right)}{\dfrac{1}{N_{up,k}} \int_0^1 I_{mn,k}\left(N_{av,k}, C_{s,k}, T, \Theta; \{p_{i,k}\}\right) dt}$$ (9)

$$N_{loss,k+1} = \frac{NINPUT}{\int_0^1 N_{av,k} \, dt}$$ (10)

where $\{p_{i,k}\}$ denotes the kth iteration of the set of calibration parameters.

The iteration equation for the $k+1$th iteration for the initial values of C_v is given by

$$C_v(0)_{k+1} = C_v(0)_k \frac{\langle C_v \rangle}{\int_0^1 C_v(t)_k \, dt} \, .$$

(11)

where $\langle C_v \rangle$ denotes the observed value given in Table 9. Similar equations are used for the other four standing crops. Equations 3 through 10 are constructed from the general form

Table 8. Steady state fluxes for calibrations used for each ecosystem. Units are given in Table 1.

System Number	Vegetation type	NINPUT	GPP[l]	NPP[l]	NUPTAKE[l]
1	Polar desert/alpine tundra	0.05[a]	255	65	0.5
2	Wet/moist tundra	0.05[a]	440	120	0.8
3	Boreal woodland	0.023[b]	456	170	1.5
4	Boreal forest	0.2[c]	550	220	2.3
5	Temperate coniferous forest	0.48[d]	2200	535	4.2
6	Arid shrubland	0.48[e]	235	110	2.7
7	Short grassland	0.6[f]	388	200	3.5
8	Tall grassland	1.0[g]	965	425	5.5[j]
9	Temperate savanna	0.52[h]	890	450	5.5
10	Temperate deciduous forest	0.6[i]	1410	650	8.0
11	Temperate mixed forest	0.6[i]	1670	650	6.5
12	Temperate broadleaved evergreen forest	0.5[j]	2000[m]	850[m]	6.0[j]
13	Mediterranean shrubland	0.19[k]	1720[m]	550[j]	14.0[j]
14	Tropical savanna	0.7[j]	1100	435[j]	10.0[j]
15	Xeromorphic woodland	0.19[k]	1720[m]	550[j]	14.0[j]
16	Tropical deciduous forest	1.5[j]	2410[n]	700[j]	27.0[o]
17	Tropical evergreen forest	2.0[j]	3200[m]	1050[j]	24.0[j]

[a]Miller et al. 1984, [b]Auclair and Rencz 1982, [c]Van Cleve et al. 1983, [d]Sollins et al. 1980, [e](Precipitation input from National Atmospheric Deposition Program (NADP 1995), fixation estimate from Bjerregaard 1971), [f](Woodmansee et al. 1978, Woodmansee 1979), [g]Woodmansee 1979, [h](Dryfall from Pratt et al. 1995, wetfall from R.L. Strassman personal communication), [i]Aber et al. 1983, [j]Raich et al. 1991, [k]NADP 1995, [l]McGuire et al. 1992 except where otherwise indicated, [m]A.D. McGuire personal communication, [n]Waring and Schlesinger 1985, [o]Ramam 1975.

$$parameter_k = \frac{Measured\ flux}{\int_T f\left(variables_{k-1}\right)dt} \tag{12}$$

where T is the time over which the flux is measured and the product ($parameter \times f$) gives the instantaneous flux in the differential equation which uses the flux in calculating the state variable. Thus for example, compare eq. 3 with eq. A.74 or compare eq. 5 with eq. A.78 and one sees that eq. 12 is the integrated form of the flux equations defining the rate of change of the state variables that is set equal to the measured fluxes.

Fluxes, state variables, and climate for calibration

The values for *NINPUT*, *GPP*, *NPP*, and *NUPTAKE* are given in Table 8. Recall that *RESPAUTO* is the difference between *GPP* and *NPP*. Values for these variables were assigned as given in the footnotes to Table 8. We usually used the values originally given by Raich et al. (1991) or McGuire et al. (1992) unless more recent information was available. In the case of *NINPUT*, Raich et al. (1991) had made estimates for the tropical

Table 9. Description of soil textures and annual averages of carbon and nitrogen pools at the study sites used for calibration. The brackets denote the time-averaged values of the bracketed variables where the time of averaging is one year. Units are given in Table 1.

System number	Soil texture description	Soil class	$\langle C_v\rangle$[n]	$\langle C_s\rangle$[n]	$\langle N_{av}\rangle$[n]	$\langle N_s\rangle$[n]	$\langle N_v\rangle$[n]
1	lithosol, rocky[a]	6	450	6000	0.4	260	6.5
2	silt[a]	3	750	18000	0.4	1100[o]	15
3	sandy clay loam to sandy loam[b]	3	2200	6000[b,p]	0.5	117[p]	24
4	silt loam[c]	3	9000	11000	0.69[q]	370[r]	24
5	silty clay loam to clay loam[d]	4	43500	19000[d]	0.9[s]	363[t]	75
6	silt loam to sandy loam[e]	2	540	10600[u]	1.6	850[u]	19.5
7	fine sandy loam[f]	3	315	3800[f]	2[v]	390[f]	8.8
8	silty clay[g]	5	650	16000[g]	4[w]	1550[w]	6[x]
9	sand[h]	1	2100	5700[h]	4.3	520[h]	16
10	sandy loam[i]	2	15500	11250	2.0	560	37
11	sandy loam[i]	2	14800	10700	2.0	530	36
12	silt loam to silty clay loam[j]	3	15000[g]	13100[y,g]	1[g]	470[z]	42[g]
13	clay[k]	5	4270[g]	11700[aa]	5[g]	950[aa]	92[g]
14	sandy[l]	1	1460[g]	7970[g]	2[bb]	375[bb]	25.5[g]
15	clay[k]	5	4270	11700[aa]	5[g]	950[aa]	92[g]
16	sandy loam to clayey loam[m]	3	11150[m]	7880[cc]	5[g]	950[cc]	168[dd]
17	clay[g]	5	22500[g]	15000[ee]	1[g]	920[ee]	298[ee]

[a]Shaver and Chapin 1991, [b]Moore 1980, [c]Vierek et al. 1983, [d]Grier and Logan 1977, [e]Caldwell et al. 1977, [f]Clark 1977, [g]Raich et al. 1991, [h]Grigal et al. 1974, [i]Bowden et al. 1991, [j]Miller and Hurst 1957, [k]Lugo and Murphy 1986, [l]Huntley and Morris 1982, [m]Bandhu 1970, [n]McGuire et al. 1992 except as noted, [o]Giblin et al. 1991, [p]Auclair and Rencz 1982, [q]Weber and Van Cleve 1984, [r]Van Cleve et al. 1983, [s]Vitousek et al. 1982, [t](Grier and Logan 1977, Sollins et al. 1980), [u]Bjerregaard 1971, [v]Woodmansee et al. 1978, [w]Risser and Parton 1982, [x]Bokhari and Singh 1975, [y](Dutch and Stout 1968, Miller and Hurst 1957, Miller 1963a, Miller 1963b), [z](Miller 1968, Miller 1963a, Miller 1963b), [aa](Lugo and Murphy 1986, Murphy and Lugo 1986), [bb]Frost 1985, [cc]Misra 1972, [dd]Ramam 1975, [ee]Klinge 1976.

systems. For the other systems we have found values for *NINPUT* from literature detailing the calibration sites or from other measurement programs.

Soil texture class and annual average state variables for carbon and nitrogen are given in Table 9. The soil texture class description was taken from the descriptions of the calibration sites as noted. Based on this description the site was assigned the soil class type number based on the classification in Tables 6 and 7. Values for the carbon and nitrogen state variables were taken from Raich et al. (1991), McGuire et al. (1992), or from the original literature detailing the calibration site.

The name, latitude, longitude, and altitude of each calibration site and the station from which climatological data was taken are given in Table 10. Often a small station would be in the immediate vicinity of the calibration site, but the station might only take

Table 10. Locations of study sites used for calibrations and locations of stations used for weather data. Under the "Variables" column, "P" refers to precipitation data; "T" refers to average monthly temperature; "E" refers to average daily maximum and minimum temperatures for each month; and "D" refers to relative humidity measurements or average dewpoint.

System Number	Calibration site	Study site latitude	Study site longitude	Elev-ation (m)	Station for weather data	Station latitude	Station longitude	Elev-ation (m)	Variables
1	Toolik Lake, Alaska[a]	68° 38' N	149° 34'W	760	Toolik Lake[o]	68° 35' N	149° 35'W	760	P, T
					Galbraith, Alaska[o]	68° 29' N	149° 29'W	820	P, T
					Toolik River[o]	68° 37' N	149° 16'W	850	T
					Fairbanks, Alaska[p]	64° 49' N	147° 52'W	133	E, D
2	Toolik Lake, Alaska[a]	68° 27' N	149° 22'W	850	Same as for 1				
3	Schefferville, Quebec Canada[b]	54° 43'N	67° 42'W	600	Knob Lake[q]	54° 48' N	66° 49' W	520	P, T, E, D
4	Bonanza Creek Experimental Forest, Alaska[c]	64° 45'N	148° 15'W	230	Fairbanks, AK[p]	64° 49' N	147° 52'W	133	P, T, E, D
5	H.J. Andrews Experimental Forest, Oregon[d]	44° 15'N	122° 20'W	550[d]	H.J. Andrews Experimental Forest, Oregon[r]	44° 15' N	122° 10' W	426	P, T, E, D
6	Curlew Valley, Utah[e]	41° 52'N	113° 05'W	1350	Snowville, UT[e]	42° 06' N	112° 47' W	1381	P, T
					Elko, NV[p]	40° 50'N	115° 47'W	1547	E, D
7	Pawnee National Grassland, Central Plains Experimental Range, CO[f]	40° 49' N	104° 46'W	1652	Pawnee National Grassland, Central Plains Experimental Range, CO[s]	40° 49' N	104° 46'W	1652	P, T, E
					Cass Filed, CO[q]	41° 37' N	104° 20'W	1472	D
					Christman, CO[q]	40° 35' N	105° 08'W	1573	D
					Cheyenne, WY[q]	41° 09' N	104° 49'W	1866	D
8	Osage Site, Adams Ranch, Osage County, OK[g]	36° 57' N	96° 33'W	392	Pawhuska, OK[p]	36° 40'N	96° 21' W		P
					Ponca City, OK[p]	36° 43' N	97° 05' W	307	P, T
					Sedan, KS[p]	37° 08' N	96° 12' W		P, T
					Phillips, OK[q]	36° 46' N	96° 01' W	218	E, D
					Strother Fld, KS[q]	37° 10' N	97° 03' W	353	E, D
					Ponca City, OK[q]	36° 43' N	97° 05' W	307	E, D

Table 10. (Continued).

System Number	Calibration site	Study site latitude	Study site longitude	Elevation (m)	Station for weather data	Station latitude	Station longitude	Elevation (m)	Variables
9	Cedar Creek Natural History Area, Minnesota[h]	45° 35'N	93° 10'W	280	Cambridge State Hospital, MN[t]	45° 34' N	93° 14' W	293	P, T, E
					Anoka Co, MN[q]	45° 08' N	93° 12' W	218	D
10	Harvard Forest, Petersham, Massachusetts[i]	42° 32'N	72° 10'W	110	Harvard Forest, Petersham, MA[u]	42° 32' N	72° 10' W	110	P, T, E
					Worcester, MA[v]	42° 11' N	72° 31' W	75	D
11	Harvard Forest, Petersham, Massachusetts[i]	42° 32'N	72° 10'W	110[i]	Same as for 10				
12	Taita Experimental Station, New Zealand[j]	41° 11'S	174° 58'E	65	Wellington, New Zealand[w]	41° 17'S	174° 46'E	126	P, T, E, D
13	Guanica State Forest Biosphere Reserve, Puerto Rico[k]	17° 55'N	66° 55'W	175	Ponce, PR[v]	18° 01'N	66° 32' W	9	T
					Ensenada, PR[v]	17°58'N	66° 55' W	10	P
					Santa Isabel, PR[v]	17° 58'N	66° 24' W	9	E, D
14	Nylsvley Provincial Nature Reserve, Transvaal, South Africa[l]	24° 39'S	28° 42'E	1100	Mosdene, South Africa (ZA)[x]	24° 35'S	28° 46' E	1097	P
					Nylstrom, ZA[x]	24° 44' S	28° 56' E	1143	T
					Wonderboom, ZA[q]	25° 39' S	28° 13' E	1250	E, D
					Pietersburg, ZA[w]	23° 51'S	29° 27' E	1242	E, D
15	Guanica State Forest Biosphere Reserve, Puerto Rico[k]	17° 55'N	66° 55'W	175[k]	Same as for 13				
16	Chakia Forest, Varanasi, India	25° 20'N	83° 00'E	350[m]	Patna, India[w]	25° 37' N	85° 10' E	53	T, P, E, D
					Allahabad, India[w]	25° 17' N	81° 44'E	98	T, P, E, D
17	Reserva Florestal Adolpho Ducke, Manaus, Brazil	2° 57'S	59° 57'W	48[n]	Manaus, Brazil[w]	3° 08' S	60° 01' W	48	T, P, E, D

[a]Shaver and Chapin 1991, [b](Auclair and Rencz 1982, Nicholson and Moore 1977), [c]Vierek et al. 1983, [d]Grier and Logan 1977, [e]Caldwell et al. 1977, [f](Clark 1977, Sims et al. 1978), [g](Conant and Risser 1974, Sims et al. 1978), [h](Ovington et al. 1963, Grigal et al. 1974), [i](Bowden et al. 1991, WeatherDisc Associates 1989), [j](Miller 1961, New Zealand Meteorological Service 1962), [k](Murphy

Table 20. Change in average sequestered carbon ΔC at steady state for each system type in vegetation and soil for specified changes in driving variables.

System Number	Nominal Carbon Storage C_v+C_s	Response of carbon storage to N_{input} e_{CN} $(10^3$ gC gN^{-1} yr)	ΔC (gC m^{-2})									
			N_{input} +10%	$T+1°C$	$T+2°C$	Dewpt +1°C	Sun hr +10%	Precip +10%	CO$_2$ +10%	2xCO$_2$	2xCO$_2$ $T+1°C$	2xCO$_2$ $T+2°C$
1	6450	39.4	197	-39	-84	-2	28	34	115	637	593	593
2	18750	51.6	258	129	-6	-37	60	-103	201	1425	1571	1636
3	8200	104.3	240	23	-32	0	28	5	138	808	859	877
4	20000	15.7	755	-696	-1378	372	80	279	462	2866	2444	2046
5	62500	36.9	1770	49	-383	691	284	438	1260	7705	8364	8582
6	11140	7.3	348	-35	-65	17	8	-33	255	1602	1637	1681
7	4115	2.4	142	16	-20	11	42	-154	105	560	600	602
8	16650	2.4	244	-815	-1660	174	-40	296	371	2077	1276	469
9	7800	2.1	108	-67	-183	-41	85	-104	143	850	830	766
10	26750	7.8	470	-130	-404	133	63	61	475	2859	2861	2736
11	25500	7.9	473	-234	-647	192	73	117	463	2787	2650	2353
12	28100	14.5	724	-138	-452	242	163	224	535	3249	3069	2762
13	15970	9.8	186	-1009	-1962	163	-201	496	338	2047	1140	273
14	9430	4.6	323	-374	-764	68	-12	260	132	882	572	260
15	15970	8.7	166	-861	-1756	144	-37	314	297	1765	984	154
16	19030	1.9	284	-1100	-2344	92	32	257	395	2454	1444	263
17	37500	5.2	1035	-760	-2062	401	-76	625	736	4476	4031	3042

and Lugo 1986, Lugo and Murphy 1986), [l]Frost 1985, [m]Bandhu 1970, [n](Roberts et al. 1990, Prance 1990, Muller 1982), [o](Haugen 1982, NCDC 1995), [p]NOAA 1974b, [q]WeatherDisc Associates 1989, [r]Bierlmaier and McKee 1989, [s]R. Harte personal communication, [t]D. Grigal personal communication, [u]LTERNet 1995, [v]NOAA 1974a, [w]Muller 1982, [x]Huntley and Morris 1982.

average monthly temperature or average monthly precipitation or sometimes both. For values of average daily maximum temperature, average daily minimum temperature, or average dewpoint, it was often necessary to use stations further removed from the calibration site. In doing so, we chose the distant site (or sites) based on the criteria for providing good interpolation, (e.g. Osage stations), for having similar climatalogical averages (e.g., Toolik Lake site), or having similar extreme statistics to that known for the calibration site (e.g., Curlew Valley site). In the specific case of the Curlew Valley site, we used Elko, NV, as the station for temperature extremes because the extremes at Elko for January and July matched quite well the known values for Curlew Valley. We used Elko even though we had data for several stations closer to the calibration site. The number of rainy days for the month was taken from a global grid constructed using the radial basis function method described by Kansa et al. (1994). Station data from WeatherDisc Associates (1989) was used in constructing the global grid of number of rainy days per month. The ratio of actual sunshine hours to possible sunshine hours for each month was taken from a gridded data base developed by Leemans and Cramer (1992). We used the value of 340 ppmv for atmospheric CO_2 concentration for calibrating the model at each site.

Response of the model to changes in model parameters and external variables

We investigate the response of the model to changes in input parameters and to changes in the environment, either climate or CO_2 level.

Sensitivity of the model at steady state to changes in model parameters.–We first ran the model with each parameter set to its nominal value. Then, one by one, we increased each parameter by 10% and ran the model to steady state to determine the new output values. We define the sensitivity Γ_{ik} of the state variable x_i to the parameter p_k by

$$\Gamma_{ik} = \frac{\dfrac{x_i\left(\left\{p_{l,nominal \atop l \neq k}, p_{k,new}\right\}\right) - x_i\left(\left\{p_{l,nominal}\right\}\right)}{x_i\left(\left\{p_{l,nominal}\right\}\right)}}{\dfrac{p_{k,new} - p_{k,nominal}}{p_{k,nominal}}} \tag{13}$$

where x_1 through x_5 is C_v, C_s, N_v, N_s, and N_{av}, respectively. For $|\Gamma_{ik}| > 1$, we consider the *i*th variable to be ultra sensitive to the *k*th parameter and, speaking colloquially, we refer to the parameter as ultra sensitive. For $|\Gamma_{ik}| \approx 1$ we consider the variable to be sensitive. For $|\Gamma_{ik}| < 0.1$, we consider the variable to be insensitive. To get an indication of the sensitivity of the system as a whole to the parameter p_k, we define the total system sensitivity $\langle \Gamma_k \rangle$ to parameter p_k to be
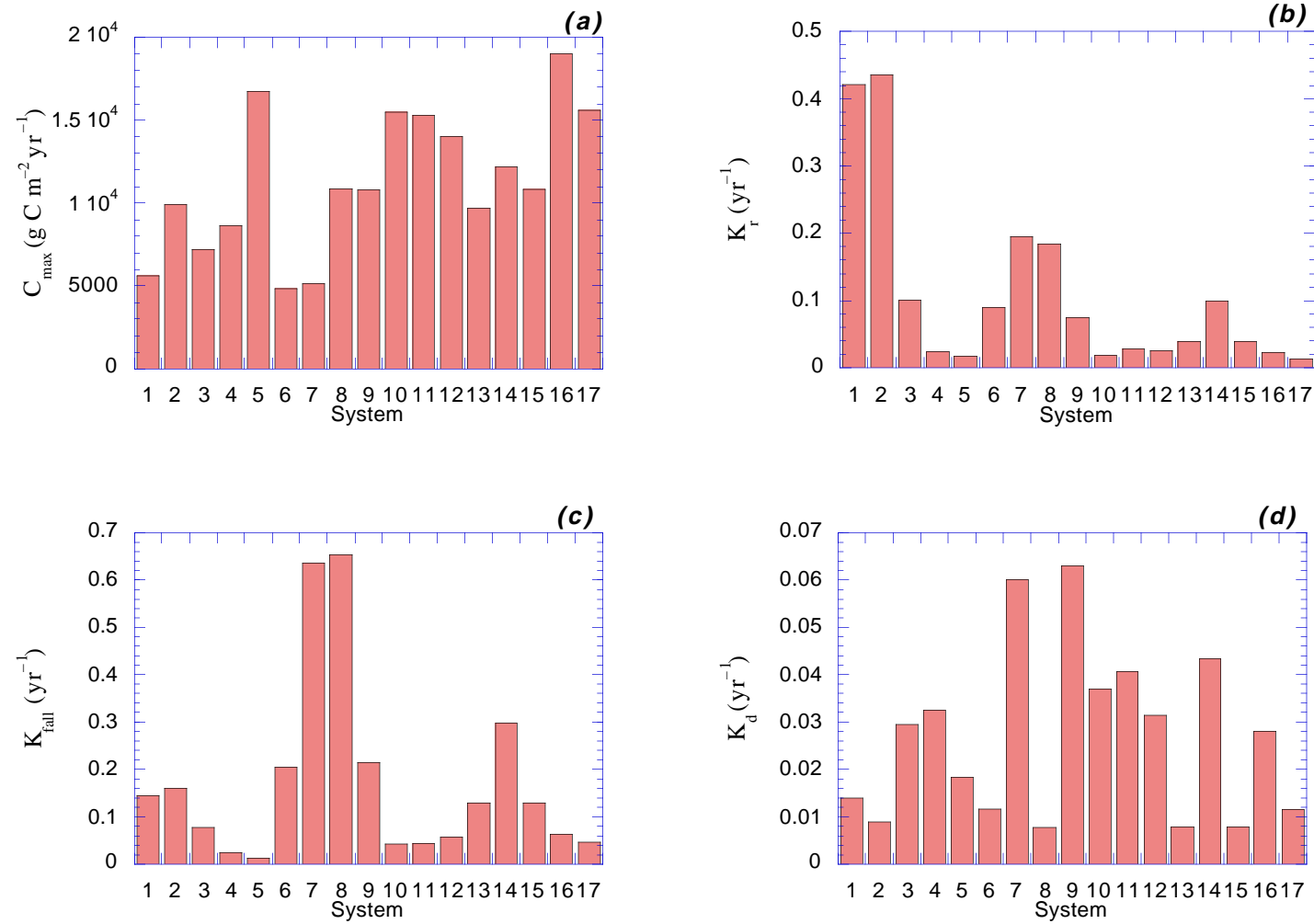
Fig. 2. Calibration results for the 17 calibration sites for the carbon-flux parameters for (a) gross primary productivity C_{max}, (b) maintenance respiration K_r, (c) carbon transfer by litterfall K_{fall}, and (d) soil respiration K_d.
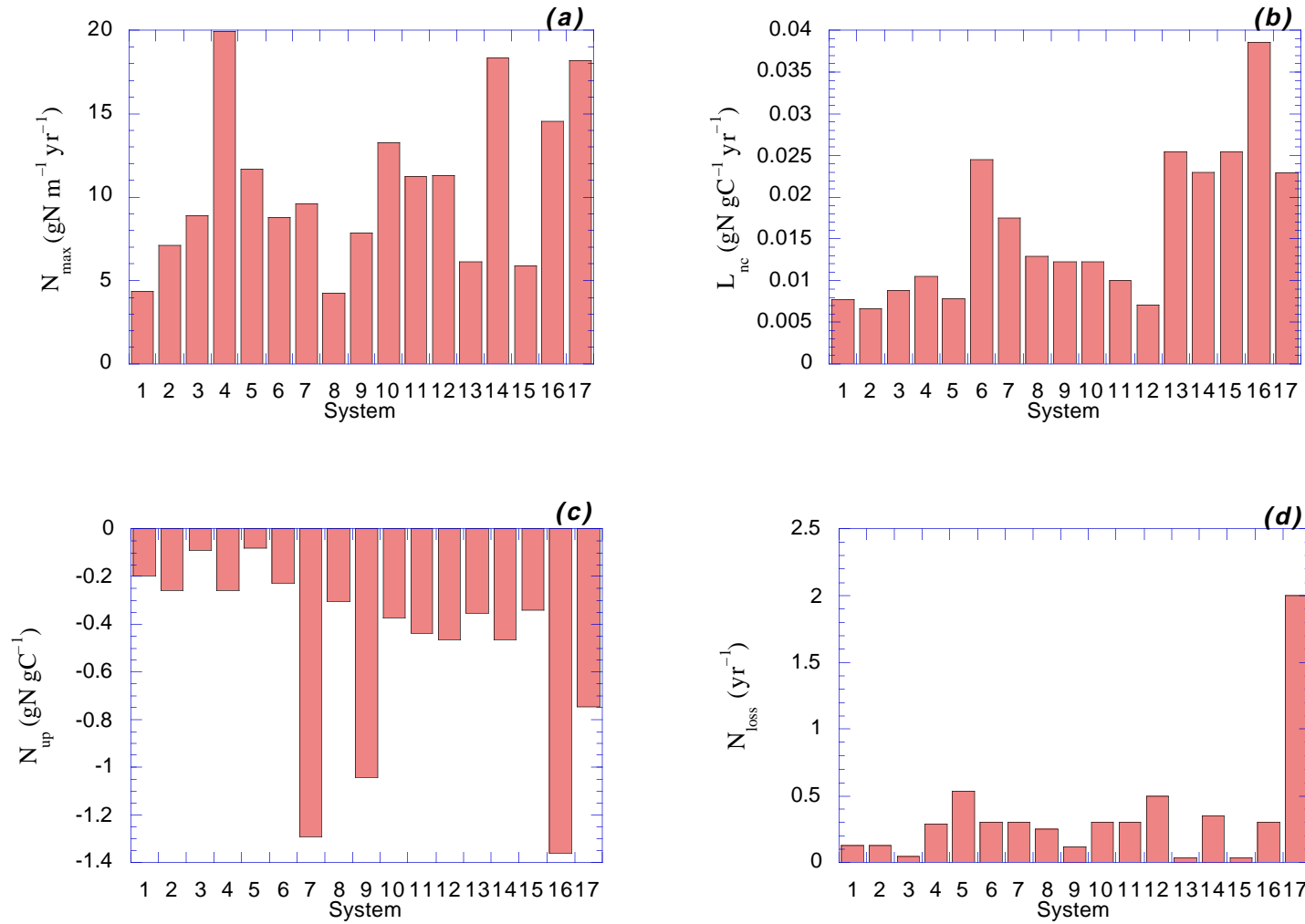
Fig. 3. Calibration results for the 17 calibration sites for the nitrogen-flux parameters for (a) uptake by vegetation N_{max}, (b) nitrogen transfer by litterfall L_{nc}, (c) uptake and immobilization of nitrogen by soil organisms N_{up}, and (d) loss of nitrogen from the ecosystem N_{loss}.

$$\langle \Gamma_k \rangle = \left[\frac{1}{5} \sum_{i=1}^{5} \Gamma_{ik}^2 \right]^{1/2} \tag{14}$$

We also calculate the net change in total carbon sequestered in vegetation and soil standing crops for a 10% change in each model parameter. In addition, we calculate the net change in net primary production for a 10% change in parameters.

Response of the steady state to changes in the environment.–We examine the effect that changes in the environment have on total carbon sequestered in vegetation and soil and on net primary productivity. As before the model is first run with nominal environmental inputs and then run again for each change in the environmental input. Results are calculated relative to the run with nominal values. Each environmental change is examined separately. The environmental changes were a 10% increase in nitrogen input, precipitation, actual sunny hours as a fraction of total possible sunny hours, and CO_2; an increase in temperature of 1˚C and 2˚C; an increase of dewpoint of 1˚C; a doubling of CO_2, and a doubling of CO_2 with a 1˚C and a 2˚C temperature increase.

Transient response to a change in temperature.–To investigate the longer term response of the model over time, we show the change in carbon in vegetation responding to a change in temperature. This calculation is done by first running the model to steady state. Then, at the beginning of year 0, temperature is abruptly changed to by 1˚C and the system is allowed to respond over time. In our simulations, we allow 500 years to elapse.

RESULTS

Parameters determined by calibration

Results for the parameters determined by calibration are shown in Figs. 2 and 3. with the numerical results in the appendix in Table A.5. The parameters determined in the calibration provide interesting details of the model's properties.

The tropical deciduous forests stand out with the highest potential gross primary productivity (C_{max}); next come the tropical evergreen forests and the three temperate forests, followed by the two savannas, tall grasslands, and xeromorphic woodland systems. The boreal systems and wet tundra come next; and the highly-stressed, arid systems (polar desert, arid shrubland, and shortgrass steppe) come last. This ranking is correlated with the *GPP* flux used in calibration.

For K_r the intrinsic rate of plant respiration, systems with large woody components (forests) have small values; systems with small or no woody components (such as grasslands) have high values. Systems that have intermediate levels of woody components (savannas, shrublands, and woodlands) have intermediate values of K_r. This demonstrates the construction of TEM, after which TERRA is patterned. This variation compensates for the simple structure (a single vegetation compartment) of the original TEM local ecosystem model. If we separate out the plant parts into leafy, bole, root components, etc., and had separate K_r for each, we should find that K_r is similar for similar components across vegetation types.

Note that the calibrated values of the litterfall turnover rate K_{fall} is low for forests, intermediate for woodland, savanna, and tundra, and high for grasslands. That is, those systems with relatively large perennial woody parts have low values whereas those systems consisting mainly of leafy parts that turn over once a year have high values. This variation also compensates for the single vegetation compartment of the local community model.

The values of the soil respiration parameter K_d for tundras, arid shrublands, xeromorphic systems and tropical evergreen forests values are relatively low while the

38

temperate systems, boreal systems, tropical savannas, and tropical deciduous forests have relatively high base rates of decomposition.

Relationship of Parameter for Gross Primary Productivity to Projected Leaf Area Index
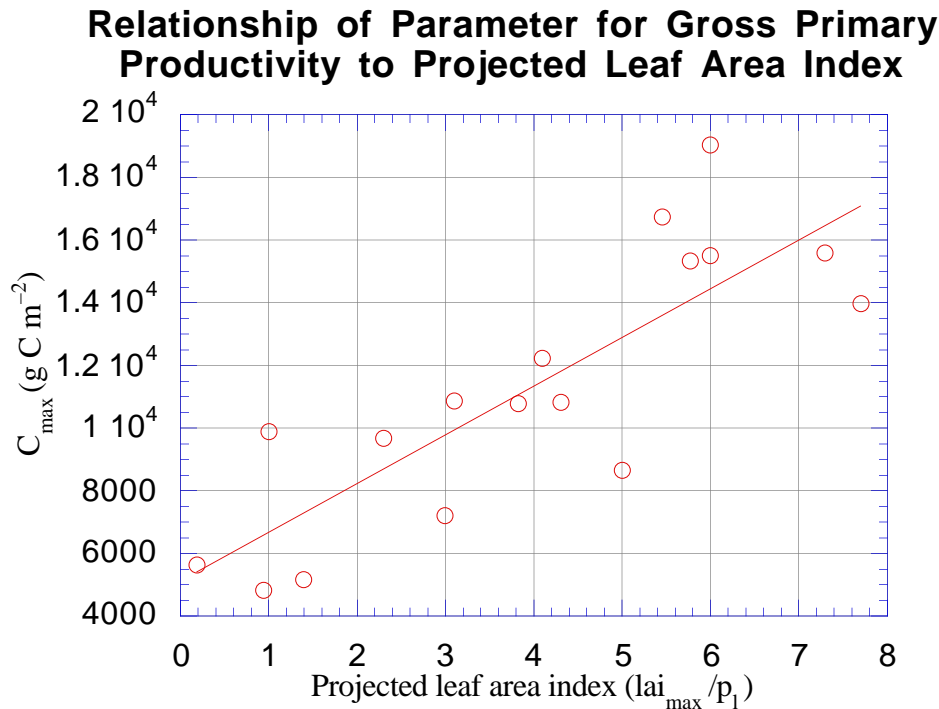
Fig. 4. Scatterplot of intrinsic base gross primary productivity (C_{max}) plotted against projected leaf area index (lai_{max}/p_l) for each of the 17 vegetation types. The linear relationship shown has an r^2 of 0.69.

       The lowest values of N_{max} are for the dry tundra, tall grass prairie, and xeromorphic systems; the highest values are for tropical systems and boreal forests with the rest of the temperate systems and boreal woodlands at intermediate to high values. The highest ratios of litter nitrogen to litter carbon (L_{nc}) are in the tropics and the lowest values are in the polar and boreal regions. The temperate systems are intermediate. Low base intrinsic factors for immobilization N_{up} occur in tundra and boreal systems; high rates occur in tropical systems with most temperate systems having intermediate values. Shortgrass steppe and temperate savannas had exceptionally high intrinsic immobilization factors. Extremely low coefficients for nitrogen loss rates N_{loss} are found for boreal woodlands and xeromorphic systems. Temperate savannas and tundra also have relatively small loss rate coefficients. Tropical evergreen rain forests has a very high loss rate coefficient. The remaining systems have intermediate values with the temperate coniferous and temperate broad-leaved evergreen forests having the highest of these intermediate values.

       The parameter C_{max} is the intrinsic rate of carbon fixation for leaf tissue. The effect of other factors on productivity such as length of the growing season, light, temperature, precipitation, the relative amount of leaf area index as a fraction of the maximum, and soil moisture are accounted for elsewhere in the model. One variable that the structure of eqs. A.74 and A.85 does not account for is the maximum leaf area index that can be attained. In Fig. 4 we show the scatter plot between C_{max} and projected maximum leaf area index lai_{max} plotted over the vegetation types. If we regard C_{max} as the dependent variable and laimax as the independent variable, a least squares fit to the data gives an intercept of 5132 gC m^{-2} yr^{-1} and a slope of 1553 gC m^{-2} yr^{-1} per unit of lai with an r^2 of 0.69.
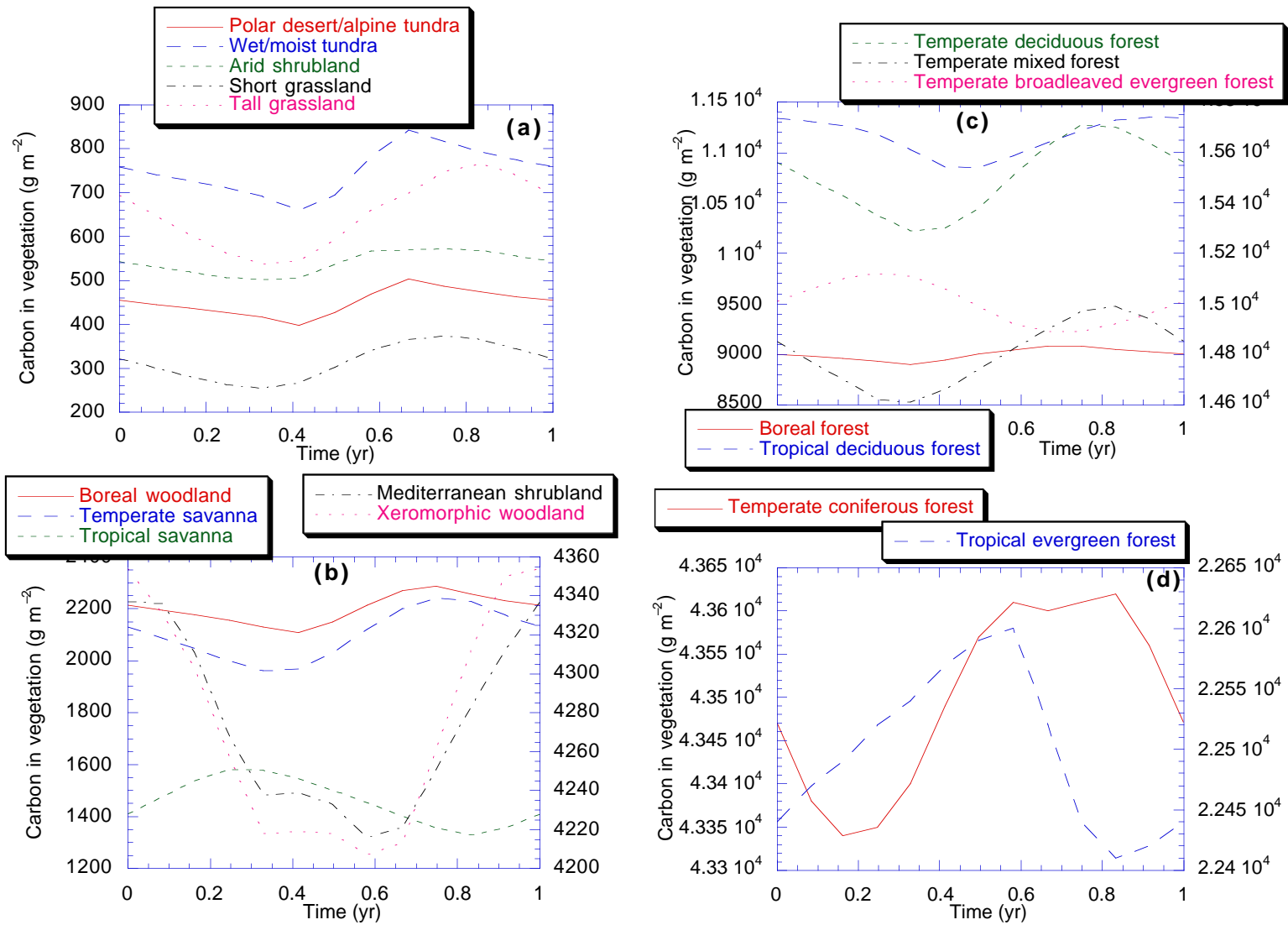
Fig. 5. Annual seasonal variation of the carbon stored in live vegetation is shown for all 17 calibrated systems. These values are for steady state conditions and for the calibration parameters given in Table A.5. Climatic conditions are from the data sets described in Table 10. Woody systems have high average levels; grasslands, tundra, and arid shrubland have low. Right hand legends refer to right-side scales.
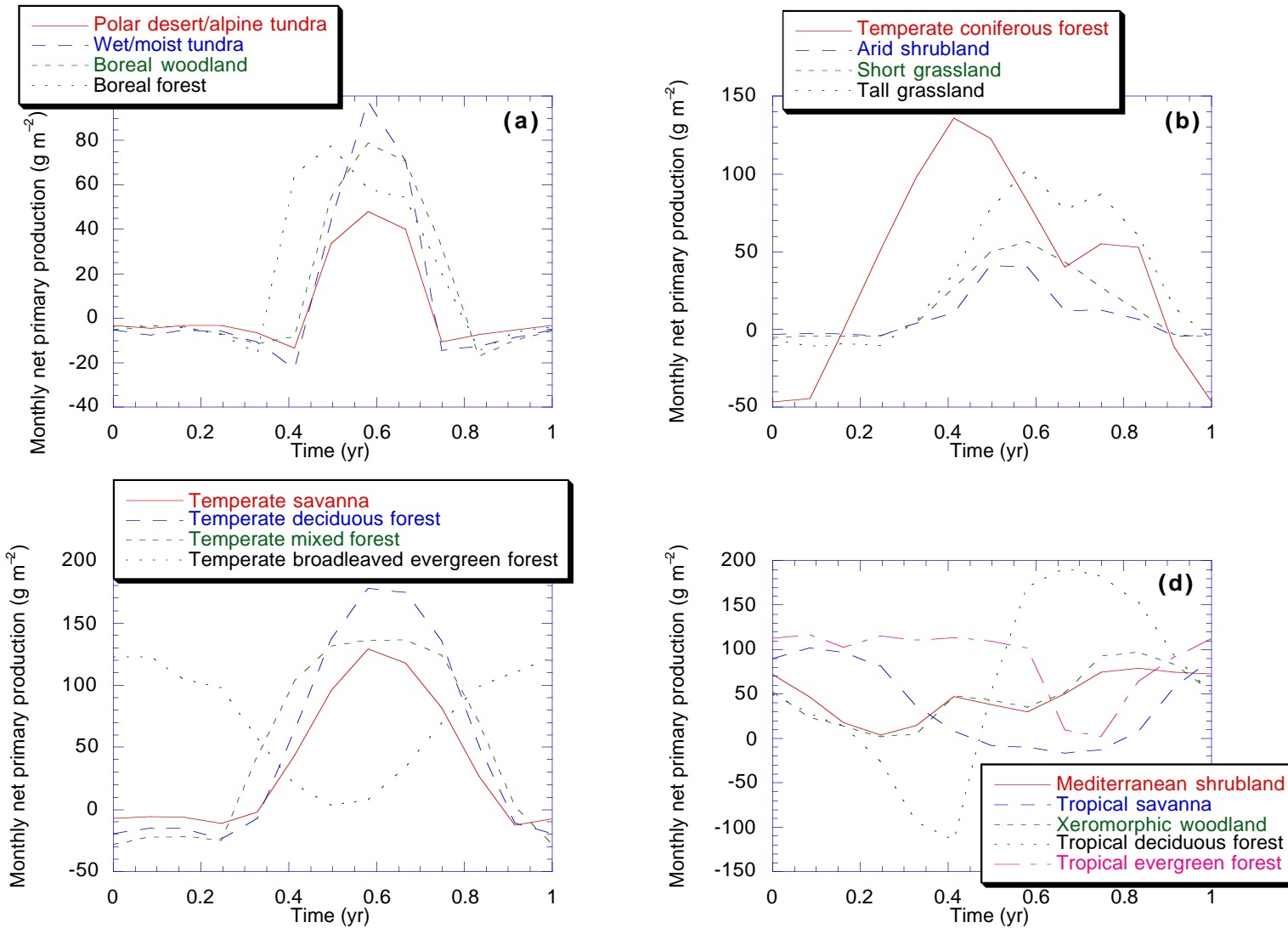
Fig. 6. We show the monthly values of net primary producitivity $(g\ m^{-2}\ mo^{-1})$ for the 17 calibration sites over the course of one year at steady state. Peaks occur at the optimal temperature-light-water growing conditions. High latitude systems are dominated by light and heat; low latitude systems by water.
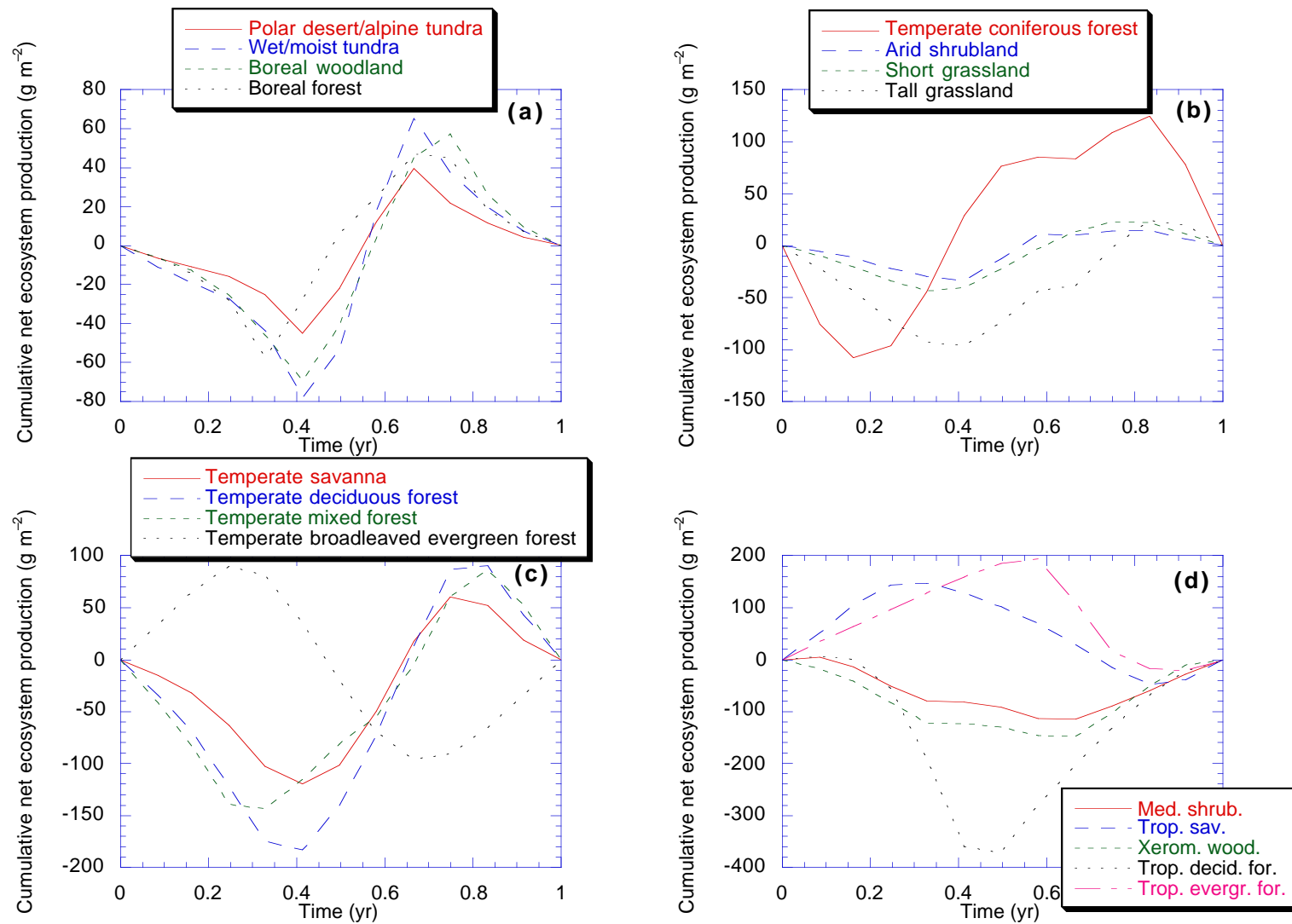
Fig. 7. Cumulative net ecosystem production is plotted for each of the 17 calibration sites. At steady state conditions, net ecosystem production begins at zero and balances back to zero by the end of the year. Peaks occur when production exceeds respiration; troughs occur for the opposite conditions.
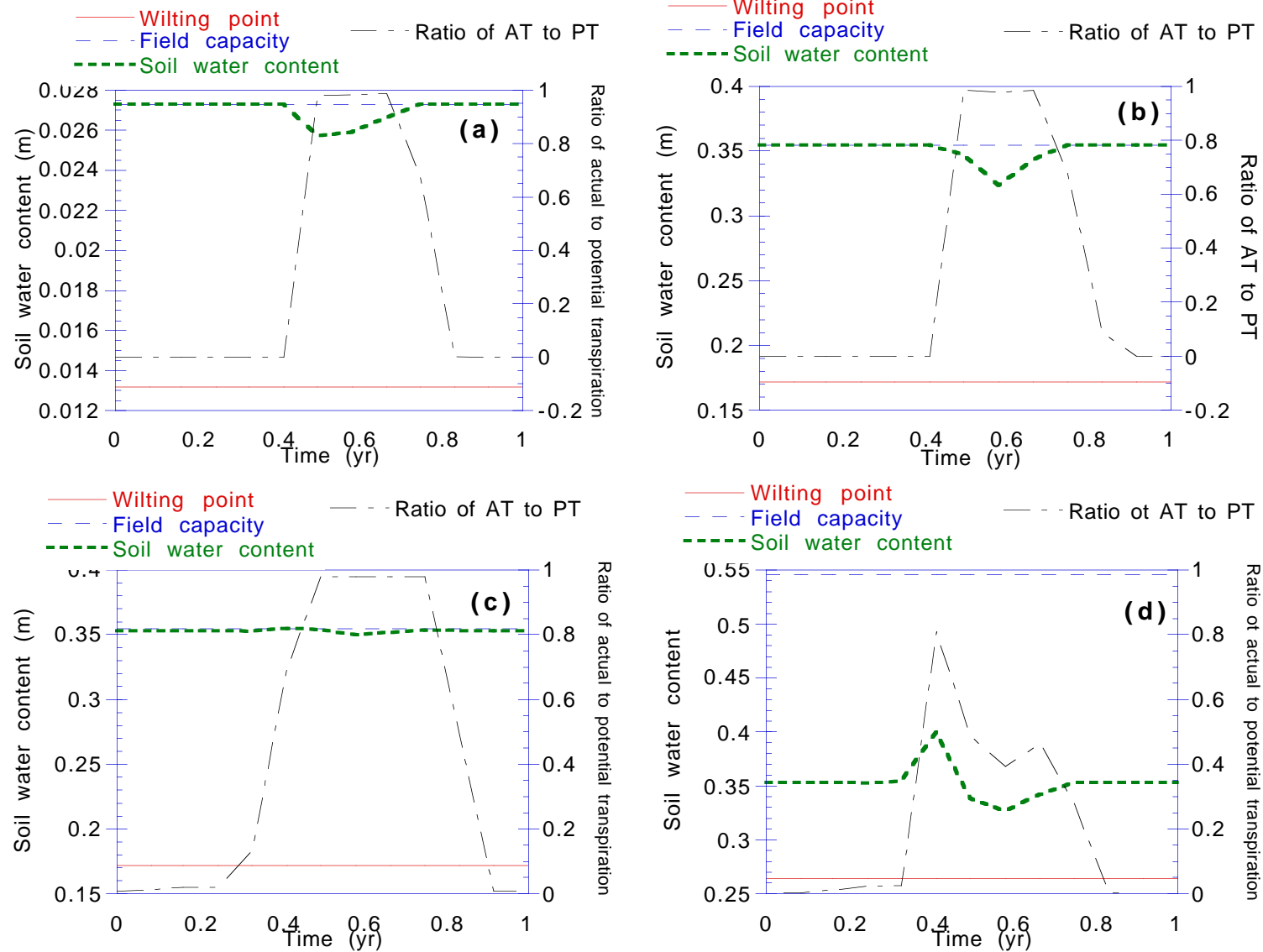
Fig. 8. The seasonal variation of soil water content and the ratio of actual (AT) to potential transpiration (PT) are plotted for (a) polar desert/alpine tundra, (b) wet/moist tundra, (c) boreal woodland, and (d) boreal forest over the course of a year. These are the same conditions as applied to Figs. 5 through 7. The ratio of AT to PT controls internal CO_2 concentration.
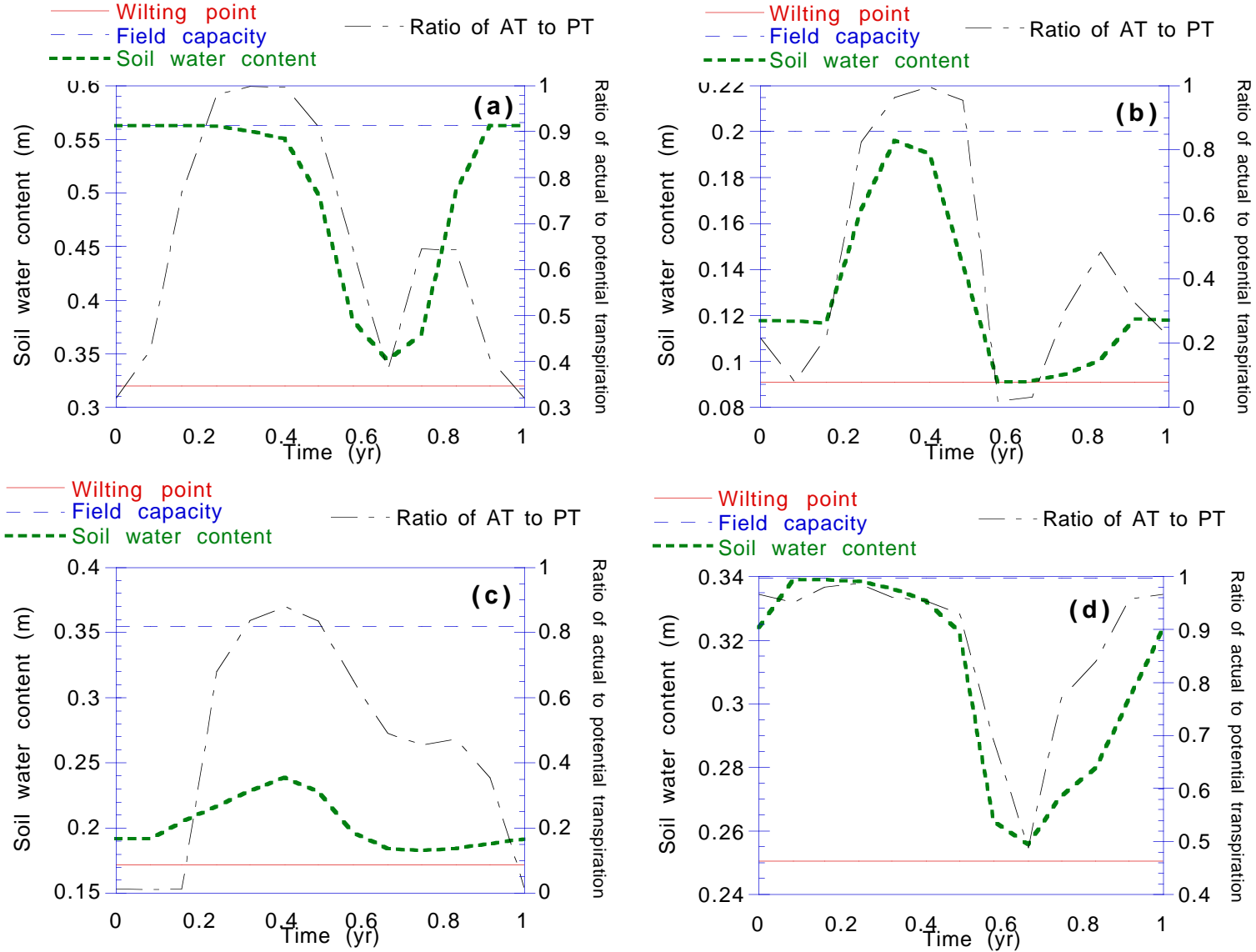
Fig. 9. The seasonal variation of soil water content and the ratio of actual to potential transpiration are plotted for (a) temperate coniferous forest, (b) arid shrubland, (c) short grassland, and (d) tall grassland over the course of a year.
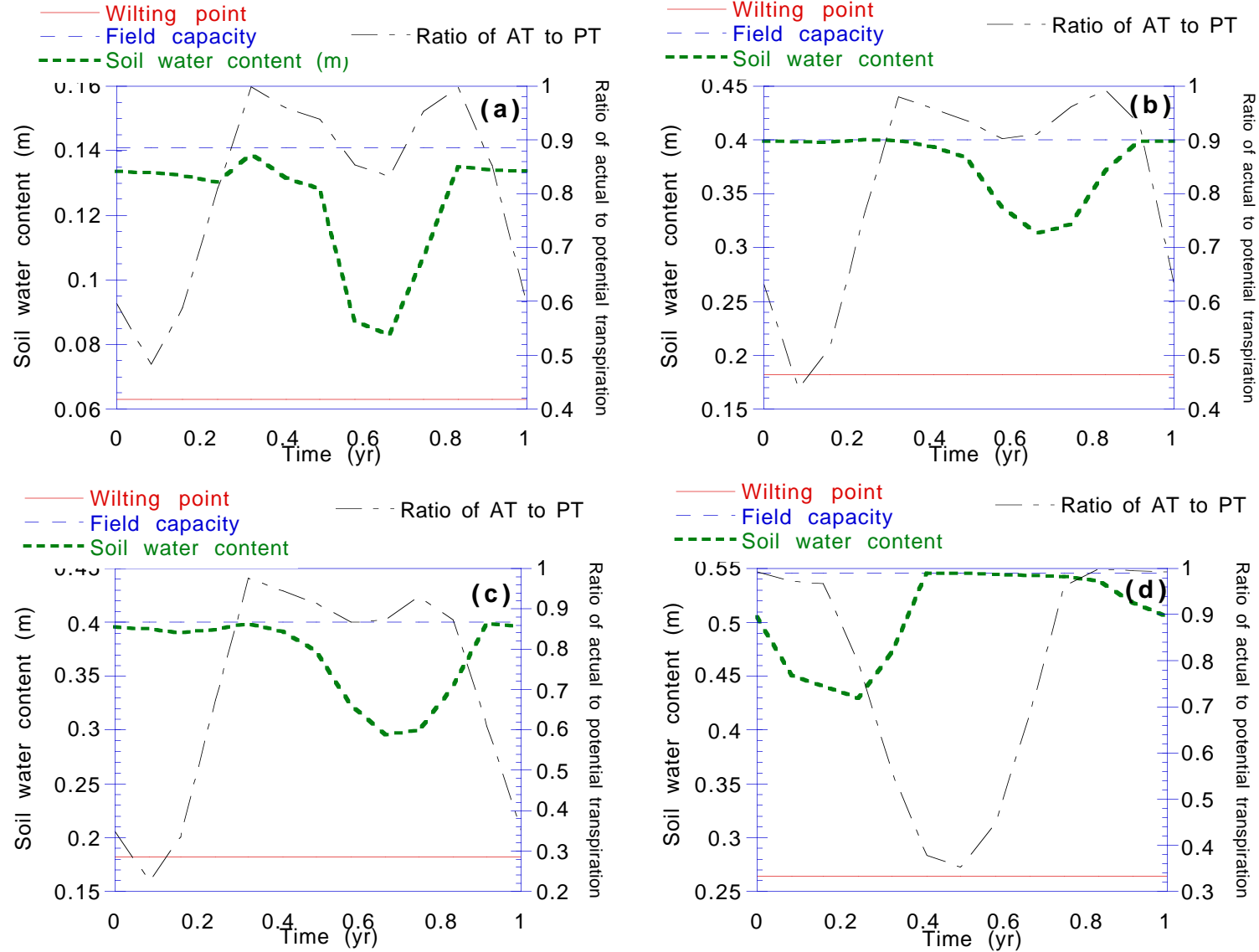
Fig. 10. The seasonal variation of soil water content and the ratio of actual to potential transpiration are plotted for (a) temperate savanna, (b) temperate deciduous forest, (c) temperate mixed forest, and (d) temperate broad-leaved evergreen forest over the course of a year. These are the same conditions as applied to Figs. 5 through 7.
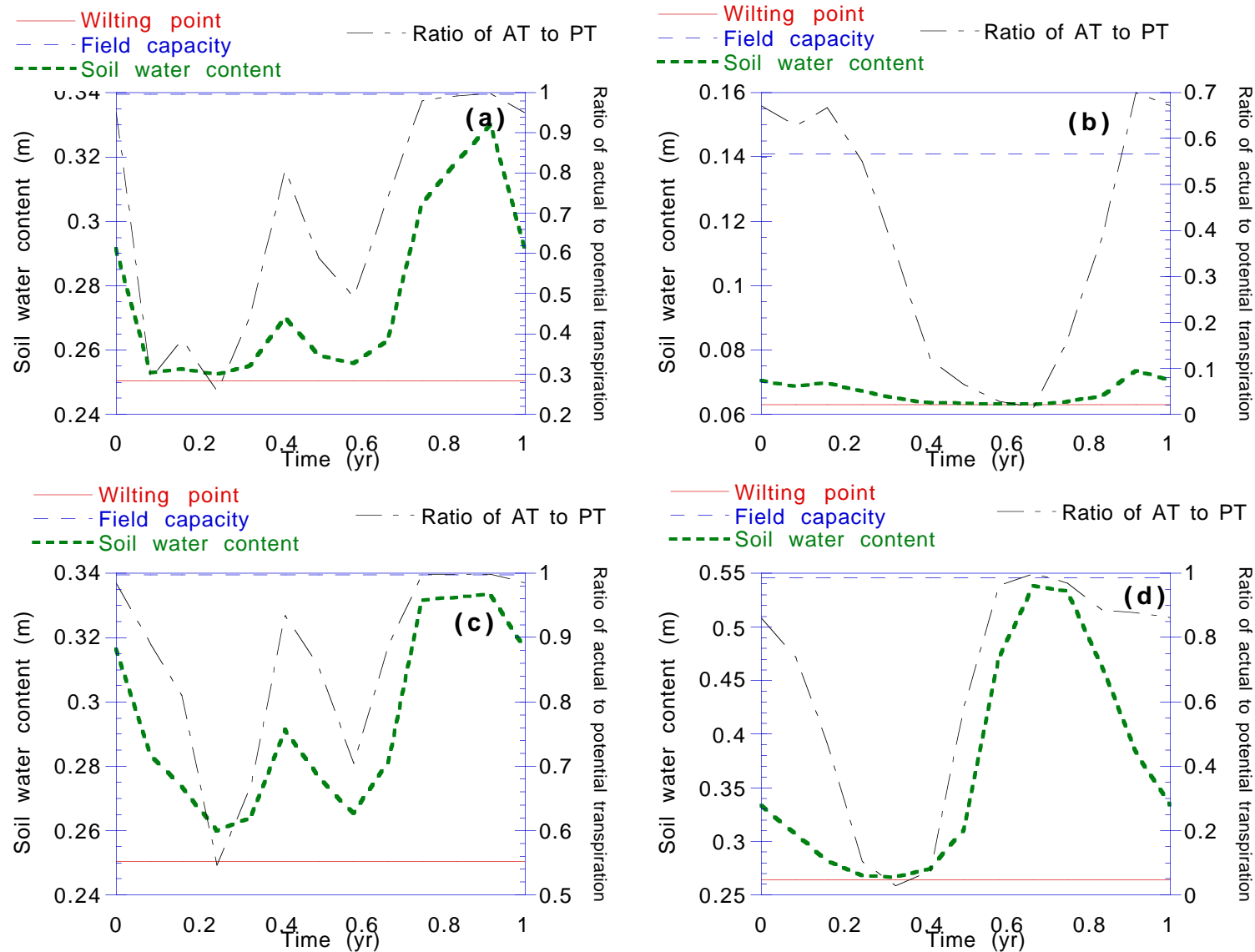
Fig. 11. The seasonal variation of soil water content and the ratio of actual to potential transpiration are plotted for (a) Mediterranean shrubland, (b) tropical savanna, (c) xeromorphic woodland, and (d) tropical deciduous forest over the course of a year. These are the same conditions as applied to Figs. 5 through 7.
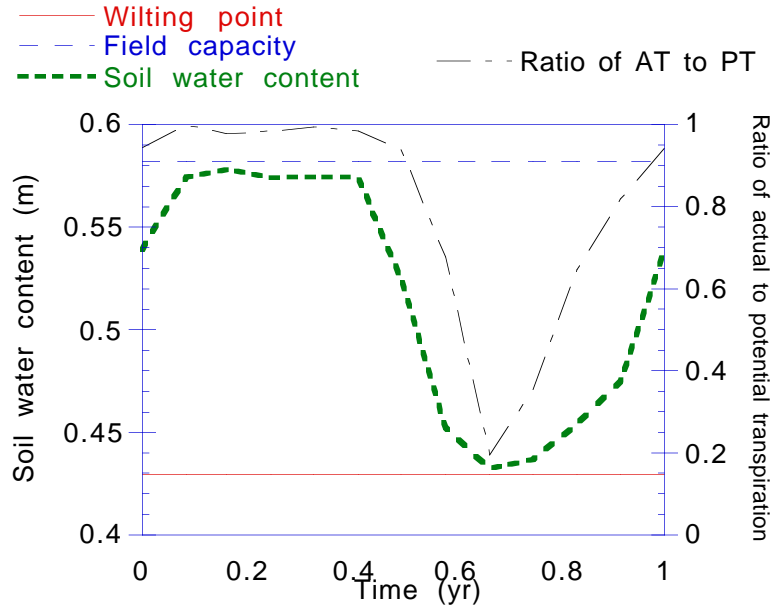
Fig. 12. Seasonal dynamics of soil water content and the ratio of actual (AT) to potential (PT) transpiration for the tropical evergreen forest site at Manaus, Brazil. The ratio of AT to PT controls internal CO_2 concentration.

Seasonal dynamics of the local ecosystem site model

We have plotted the seasonal dynamics of the carbon in vegetation C_v, monthly net primary production, and cumulative net ecosystem production for the seventeen vegetation types in Figs. 5, 6, and 7, respectively. The seasonal dynamics of soil water and the ratio of actual to potential transpiration is plotted for the seventeen vegetation types in Figs. 8 through 12.

Seasonal behavior of carbon in vegetation.–We see in Fig. 5 that the systems limited by low temperature and short growing seasons (tundra and boreal) reach their peak standing crops relatively early in the year. The short grassland site has about one half the biomass of the tall grassland site and the tall grassland site reaches its peak standing crop later in the year than the short grassland site. The amplitude of the arid shrubland is smaller than the amplitudes of the other water- or cold-limited systems. The tropical savanna site in southern Africa has almost exactly the opposite annual phase as the temperate savanna site in Minnesota. The differences between the parameters for the Mediterranean shrubland and for the xeromorphic woodland are in a_{leaf}, b_{leaf}, and c_{leaf} and parameters in the water balance submodel, lai_{max}, k_{can}, cn_{max}, s_{ahd}, and ahd_t. These differences produce a somewhat different set of calibration parameters and a somewhat different response to water stress. The temperate broad-leaved evergreen forest site in New Zealand has the opposite annual phase with less amplitude as the temperate forests in Massachusetts. The bottom of the trough in C_v at the tropical deciduous forest site in India comes at the end of the dry season; likewise, for tropical evergreen forest site in the Amazon. In the temperate coniferous forest site , the trough in C_v comes in winter around the end of February. In the temperate deciduous forest site in Massachusetts, the minimum comes around the end of April.

The simulation of litterfall could be made more realistic in deciduous systems by forcing it to occur as an event with a short time duration. This would produce curves of C_v with faster changes during those times of year in which the system undergoes litterfall. If litter and soil were treated separately and if litterfall were treated more as an event and less

as a continuous process, then somewhat different dynamics of soil and litter respiration and gas exchange might occur. This modification is an area for future research.

   Seasonal dynamics of net primary production. We define the monthly net primary production as

$$npp_{mo} = \int_{jd(mo-1)/365}^{jd(mo)/365} \left(gpp - r_m - r_g \right) dt \qquad (15)$$

where $jd(mo)$ is the Julian day of the last day of the month *mo*, *t* is the time in years, and the other variables are as defined in Table 1. In Fig. 6, the high latitude systems (tundra and boreal) show a widening of the growing season going from tundra to boreal woodland to boreal forest. The boreal forest site was quite dry, hence the dip in *npp* late in the growing season. The temperate coniferous forest site has relatively mild winters, early spring, and relatively dry summers. The fall rains and mild temperatures produce late season production. The arid shrubland has a relatively short production season peaking earlier than either the short or tall grassland. The tall grassland site is more productive with a longer growing season than the short grassland site. The two north American temperate sites in Minnesota and Massachusetts have similar timing of their peaks in production, but the Massachusetts site has a longer growing season. The tropical broad-leaved evergreen forest site has the annual production cycle almost exactly of opposite phase compared to the north American sites. The Mediterranean shrubland and xeromorphic woodland vegetation types have very similar production responses to the Puerto Rican site. The tropical savanna production cycle in southern Africa has almost the opposite phase to that of the temperate savanna in Minnesota. The production cycle in the tropical deciduous forest in India is controlled by the monsoon. The tropical evergreen forest site in the Amazon shows a strong dip during the summer dry season. In general, we see cold temperatures controlling or limiting high latitude systems, precipitation controlling tropical systems, and a mix of temperature and rainfall controlling temperate systems.

   Seasonal dynamics of net ecosystem production (*net gas exchange*).–In Fig. 7, we show the response of cumulative net ecosystem production over the months of the year for the seventeen calibration systems. Cumulative net ecosystem production is defined as

$$nep_{mo} = \int_{0}^{jd(mo)/365} \left(gpp - r_m - r_g - r_H \right) dt. \qquad (16)$$

If we momentarily ignore atmospheric transport, the quantity ($-nep_{mo}$) follows the seasonal fluctuation of atmospheric CO_2 just above the canopy. We can see that the high latitude and northern hemispheric temperate sites show a trough in *nep* early in the year and a peak later in the year. The relative sizes of the troughs and peaks and the timing of troughs and peaks for these systems vary from site to site depending on the details of climate and system response. Notice the relatively early trough for the temperate coniferous forest site and relatively late trough for the temperate savanna site and temperate deciduous forest system. The temperate mixed forest shows a trough at an earlier time in the spring than the temperate deciduous forest. Just past the bottom of the trough is when production begins to exceed respiration. This occurs earlier for the temperate mixed forest than for the temperate deciduous forest. Note that these two systems are both at the same calibration site. The differences in timing of production and respiration are therefore differences in system response rather than differences in the underlying climate or soil.

   In Fig. 8, we show the soil water content and the ratio of actual to potential transpiration for the tundra and boreal systems. Recall that the ratio of actual to potential transpiration is the variable used to couple the water relations submodel to the gross

primary production calculation in the TEM submodel. This ratio is roughly proportional to

Table 11. Sensitivity of the total system $\langle \Gamma_k \rangle$ for a change of 10% in each parameter for systems 1 through 6. This unitless number is the relative change in standing crops per relative change in parameter averaged over the five carbon and nitrogen components of the ecosystem.

System 1	$\langle \Gamma_k \rangle$	System 2	$\langle \Gamma_k \rangle$	System 3	$\langle \Gamma_k \rangle$	System 4	$\langle \Gamma_k \rangle$	System 5	$\langle \Gamma_k \rangle$	System 6	$\langle \Gamma_k \rangle$
m_{opt}	1.24	m_{opt}	1.327	m_{opt}	1.329	m_{opt}	4.851	m_{opt}	2.821	m_{opt}	3.027
fc_{sat}	0.96	fc_{sat}	1.001	fc_{sat}	0.844	fc_{sat}	0.953	fc_{sat}	0.863	fc_{sat}	0.661
fc_{sv}	0.78	pv_{sv}	0.746	K_d	0.620	$msat$	0.868	K_d	0.716	K_d	0.634
pv_{sv}	0.60	fc_{sv}	0.701	fc_{sv}	0.577	pv_{sv}	0.723	Q_{10}	0.690	Q_{10}	0.629
K_d	0.57	K_d	0.548	K_{fall}	0.575	K_d	0.693	pv_{sv}	0.566	$msat$	0.627
K_{fall}	0.52	K_{fall}	0.542	pv_{sv}	0.512	N_{loss}	0.604	N_{loss}	0.530	N_{loss}	0.561
N_{loss}	0.45	V_{cn}	0.412	L_{nc}	0.430	Q_{10}	0.475	fc_{sv}	0.494	T_{opt}	0.507
V_{cn}	0.43	N_{up}	0.354	V_{cn}	0.423	K_{fall}	0.473	K_{fall}	0.438	K_{fall}	0.485
a_{leaf}	0.36	L_{nc}	0.334	N_{max}	0.325	wp_{sv}	0.443	N_{max}	0.420	pv_{sv}	0.457
N_{max}	0.35	N_{max}	0.320	C_{max}	0.315	V_{cn}	0.417	C_{max}	0.419	T_{min}	0.438
C_{max}	0.35	C_{max}	0.311	T_{opt}	0.298	N_{max}	0.404	V_{cn}	0.412	V_{cn}	0.412
L_{nc}	0.33	T_{opt}	0.237	N_{loss}	0.287	C_{max}	0.402	$msat$	0.396	N_{max}	0.406
N_{up}	0.30	k_{n1}	0.233	ml	0.286	L_{nc}	0.371	L_{nc}	0.373	C_{max}	0.405
ml	0.26	k_{n2}	0.229	$cldsoil$	0.285	k_{n1}	0.322	K_r	0.295	L_{nc}	0.364
k_{n1}	0.24	K_r	0.228	s_{nt}	0.284	N_{up}	0.283	T_{min}	0.293	k_{n1}	0.281
K_r	0.23	N_{loss}	0.164	s_{td}	0.283	fc_{sv}	0.265	T_{opt}	0.266	N_{up}	0.264
T_{opt}	0.23	k_{lsr}	0.161	T_{tcd}	0.281	lai_{max}	0.222	N_{up}	0.262	wp_{sv}	0.234
c_1	0.21	T_{min}	0.148	ahd_t	0.281	k_{n2}	0.209	k_{n1}	0.258	lai_{max}	0.224
T_{min}	0.21	$adapt$	0.136	c_1	0.271	cn_{max}	0.204	wp_{sv}	0.251	mst_{mn}	0.211
b_{leaf}	0.21	a_{leaf}	0.132	c_2	0.269	K_r	0.194	k_{lsr}	0.206	k_{CO2}	0.199
k_{n2}	0.20	$c1$	0.132	Q_{10}	0.259	k_{CO2}	0.194	k_{CO2}	0.182	K_r	0.167
T_{max}	0.19	dcE	0.130	k_{lsr}	0.255	ml	0.189	lai_{max}	0.169	cn_{max}	0.163
c_2	0.18	S_p	0.129	rt	0.248	k_{lsr}	0.180	cn_{max}	0.152	k_{n2}	0.158
min_{leaf}	0.15	Q_{10}	0.128	k_{n1}	0.248	mst_{mn}	0.167	k_{n2}	0.140	ml	0.114
Q_{10}	0.14	min_{leaf}	0.122	wp_{sv}	0.246	$cldsoil$	0.130	S_p	0.133	K_{min}	0.112
cl_{eaf}	0.14	lai_{max}	0.122	$msat$	0.245	T_{opt}	0.116	k_{lgt}	0.112	k_{lsr}	0.098
k_{CO2}	0.14	k_{CO2}	0.121	S_p	0.243	T_{min}	0.115	τ	0.111	T_{max}	0.094

leaf conductivity. We see that the tundra sites and the boreal woodland site are quite wet. The boreal forest site has relatively little precipitation and soil water content is low. In Fig. 9, we show the results for the temperate coniferous forest, arid shrubland, short grassland and tall grassland. The temperate coniferous forest reaches soil saturation during the winter months and then experiences drying during the summer when there is very little precipitation. The arid shrubland and tall grassland sites also dry out during summer. The short grassland site is dry but does not exercise quite the severe level of stress that the arid shrubland site undergoes. In Fig. 10, the temperate savanna becomes drier than the temperate deciduous forest and temperate mixed forest. The temperate broad-leaved evergreen forest of New Zealand undergoes reduction of conductivity during the winter of the southern hemisphere. The soil moisture draw down for the temperate broad-leaved evergreen forest is similar to those of the temperate deciduous forest and temperate mixed forest. In Fig. 11, the soil moisture response of the Mediterranean shrubland system and the xeromorphic woodland system to the Puerto Rican coastal climate pattern are similar, but some differnces in the details are evident. The Mediterranean system dries out somewhat more. The xeromorphic woodland system conserves water somewhat better. The tropical savanna is very dry. Conductivity is minimum during the southern hemisphere winter which coincides with minimum soil water. The soil water dynamics of the tropical deciduous forest of India is driven by the monsoon. Note the dry period during March, April, and May. The monsoon occurs in late summer or early fall. Soil moisture results for the tropical evergreen forest site is shown in Fig. 12. This site has a

Table 12. Sensitivity of the total system $\langle \Gamma_k \rangle$ for a change of 10% in each parameter for systems 7 through 12. This unitless number is the relative change in standing crops per relative change in parameter averaged over the five carbon and nitrogen components of the ecosystem.

System 7	$\langle \Gamma_k \rangle$	System 8	$\langle \Gamma_k \rangle$	System 9	$\langle \Gamma_k \rangle$	System 10	$\langle \Gamma_k \rangle$	System 11	$\langle \Gamma_k \rangle$	System 12	$\langle \Gamma_k \rangle$
m_{opt}	7.91	Q_{10}	1.42	m_{opt}	5.55	m_{opt}	4.37	m_{opt}	5.09	m_{opt}	4.01
$msat$	1.26	K_d	0.79	Q_{10}	1.11	Q_{10}	1.09	Q_{10}	1.16	Q_{10}	1.02
pv_{sv}	1.07	fc_{sv}	0.66	K_d	0.97	K_d	0.87	K_d	0.90	fc_{sat}	0.93
Q_{10}	1.03	m_{opt}	0.53	pv_{sv}	0.90	fc_{sat}	0.66	pv_{sv}	0.71	K_d	0.91
K_d	0.87	fc_{sat}	0.48	fc_{sv}	0.74	pv_{sv}	0.66	fc_{sat}	0.70	pv_{sv}	0.54
wp_{sv}	0.80	K_{fall}	0.47	$msat$	0.60	fc_{sv}	0.57	fc_{sv}	0.65	N_{loss}	0.54
fc_{sat}	0.72	N_{loss}	0.44	k_{lsr}	0.53	K_{fall}	0.48	N_{loss}	0.48	K_{fall}	0.47
N_{loss}	0.58	C_{max}	0.43	K_{fall}	0.49	N_{loss}	0.47	$msat$	0.47	fc_{sv}	0.46
K_{fall}	0.49	N_{max}	0.42	fc_{sat}	0.47	N_{max}	0.43	K_{fall}	0.46	k_{lsr}	0.45
C_{max}	0.43	V_{cn}	0.41	N_{loss}	0.45	C_{max}	0.42	k_{lsr}	0.44	T_{opt}	0.43
N_{max}	0.42	L_{nc}	0.40	N_{max}	0.42	V_{cn}	0.41	N_{max}	0.42	N_{max}	0.42
V_{cn}	0.41	N_{up}	0.39	C_{max}	0.42	k_{lsr}	0.41	C_{max}	0.42	C_{max}	0.42
k_{lsr}	0.40	$pvsv$	0.36	V_{cn}	0.41	L_{nc}	0.38	V_{cn}	0.41	V_{cn}	0.41
L_{nc}	0.37	k_{lsr}	0.30	a_{leaf}	0.40	$msat$	0.38	L_{nc}	0.39	L_{nc}	0.38
T_{opt}	0.37	K_r	0.19	lai_{max}	0.40	N_{up}	0.33	lai_{max}	0.38	N_{up}	0.35
N_{up}	0.36	k_{CO2}	0.19	L_{nc}	0.40	a_{leaf}	0.29	cn_{max}	0.36	$msat$	0.29
mst_{mn}	0.34	T_{opt}	0.18	S_p	0.39	lai_{max}	0.20	N_{up}	0.35	k_{n1}	0.23
k_{n1}	0.28	wp_{sv}	0.15	cn_{max}	0.38	cn_{max}	0.20	K_r	0.22	lai_{max}	0.23
b_{leaf}	0.23	lai_{max}	0.13	N_{up}	0.38	K_r	0.18	k_{n1}	0.18	cn_{max}	0.20
lai_{max}	0.23	$msat$	0.12	T_{opt}	0.25	S_p	0.18	c_{leaf}	0.18	K_r	0.20
k_{n2}	0.21	k_{n1}	0.11	τ	0.24	k_{n1}	0.17	S_p	0.18	T_{min}	0.19
T_{min}	0.20	k_{lgt}	0.10	β	0.24	k_{CO2}	0.17	a_{leaf}	0.16	k_{n2}	0.18
cn_{max}	0.19	k_{n2}	0.10	c_2	0.22	k_{n2}	0.12	b_{leaf}	0.16	S_p	0.17
k_{CO2}	0.19	cn_{max}	0.08	ml	0.18	τ	0.12	k_{n2}	0.14	k_{CO2}	0.17
S_p	0.18	T_{min}	0.08	b_{leaf}	0.17	β	0.11	T_{min}	0.14	τ	0.14
fc_{sv}	0.16	pl	0.07	c_1	0.17	b_{leaf}	0.11	τ	0.11	k_{lgt}	0.12
K_{min}	0.15	r_{grfc}	0.07	k_{CO2}	0.17	k_{lgt}	0.10			β	0.11

pronounced dry season during the summer. Note the sharp decrease in the ratio of actual to potential transpiration. This will produce a corresponding decrease in gross primary production.

Sensitivity of the model to changes in parameters

  Sensitivity of the total ecosystem.–In Tables 11, 12, and 13, we show the sensitivity $\langle \Gamma_k \rangle$ at steady state to changes for the 27 most important model parameters out of the total number of 62 parameters. The subscript k refers to the kth parameter. The statistic $\langle \Gamma_k \rangle$ is defined in eqs. 13 and 14. Tables 11, 12, and 13 show the sensitivities for systems 1 through 6, systems 7 through 12, and systems 13 through 17, respectively. In each case, we increase each parameter by 10% of its nominal value. With only a few exceptions, the systems are ultra sensitive to m_{opt} from the tundra to the tropics. This parameter is the optimum soil moisture at which decomposition respiration is maximum. Note that the exponent B in eq. A.80 and A.81 can undergo relatively large percentage changes if both m_{opt} changes and the soil water M is close to the value of m_{opt}. Other parameters in the soil water submodel, field capacity as a percent of saturation, field capacity as a fraction of soil volume, and pore volume as a fraction of soil volume, i.e., fc_{sat}, fc_{sv}, and pv_{sv}, are usually important parameters across the 17 sites. The two

Table 13. Sensitivity of the total system $\langle \Gamma_k \rangle$ for a change of 10% in each parameter for systems 13 through 17. This unitless number is the relative change in standing crops per relative change in parameter averaged over the five carbon and nitrogen components of the ecosystem.

System 13	$\langle \Gamma_k \rangle$	System 14	$\langle \Gamma_k \rangle$	System 15	$\langle \Gamma_k \rangle$	System 16	$\langle \Gamma_k \rangle$	System 17	$\langle \Gamma_k \rangle$
Q_{10}	1.812	m_{opt}	3.945	Q_{10}	1.813	m_{opt}	5.658	Q_{10}	1.889
m_{opt}	1.373	Q_{10}	1.269	K_d	0.815	Q_{10}	2.008	fc_{sv}	0.969
K_d	0.814	$msat$	0.833	fc_{sv}	0.516	pv_{sv}	1.118	fc_{sat}	0.878
K_{fall}	0.466	K_d	0.760	m_{opt}	0.473	K_d	0.912	K_d	0.843
C_{max}	0.418	N_{loss}	0.563	K_{fall}	0.459	$msat$	0.804	pv_{sv}	0.733
N_{max}	0.417	fc_{sat}	0.554	N_{max}	0.419	fc_{sv}	0.512	m_{opt}	0.682
N_{loss}	0.416	K_{fall}	0.465	C_{max}	0.418	wp_{sv}	0.497	N_{loss}	0.538
Vcn	0.406	wp_{sv}	0.433	N_{loss}	0.409	k_{lsr}	0.447	K_{fall}	0.451
fc_{sat}	0.394	pv_{sv}	0.430	Vcn	0.405	N_{loss}	0.446	N_{max}	0.423
L_{nc}	0.385	N_{max}	0.418	L_{nc}	0.385	K_{fall}	0.444	C_{max}	0.422
b_{leaf}	0.379	C_{max}	0.418	fc_{sat}	0.369	N_{max}	0.426	Vcn	0.406
pv_{sv}	0.373	Vcn	0.410	k_{lsr}	0.332	C_{max}	0.425	L_{nc}	0.375
k_{lsr}	0.331	$moist_{min}$	0.401	N_{up}	0.301	fc_{sat}	0.408	k_{lsr}	0.366
N_{up}	0.300	T_{opt}	0.394	K_r	0.255	Vcn	0.405	wp_{sv}	0.294
r_{grfc}	0.265	L_{nc}	0.372	pv_{sv}	0.244	L_{nc}	0.384	N_{up}	0.282
K_r	0.254	ml	0.334	r_{grfc}	0.219	b_{leaf}	0.310	K_r	0.256
k_{CO2}	0.189	k_{n1}	0.312	k_{CO2}	0.169	N_{up}	0.305	k_{n1}	0.254
S_p	0.164	k_{lsr}	0.262	wp_{sv}	0.164	K_r	0.276	k_{CO2}	0.183
cn_{max}	0.143	N_{up}	0.227	k_{lgt}	0.102	$moist_{min}$	0.210	$msat$	0.159
$wpsv$	0.140	Kr	0.217	k_{n1}	0.095	S_p	0.201	k_{n2}	0.155
lai_{max}	0.137	b_{leaf}	0.210	cn_{max}	0.090	k_{CO2}	0.192	lai_{max}	0.117
τ	0.117	K_{min}	0.175	lai_{max}	0.086	a_{leaf}	0.170	T_{opt}	0.109
a_{leaf}	0.116	k_{n2}	0.146	$msat$	0.084	k_{n1}	0.145	k_{lgt}	0.107
k_{n1}	0.105	k_{CO2}	0.129	b_{leaf}	0.074	lai_{max}	0.128	b_{leaf}	0.097
β	0.103	lai_{max}	0.118	k_{n2}	0.066	β	0.125	al_{eaf}	0.096
k_{lgt}	0.101	k_{lgt}	0.094	cld_2	0.062	τ	0.123	cn_{max}	0.087
$c2$	0.095	cn_{max}	0.083	r_a	0.052	cn_{max}	0.117	cld_1	0.062

different parameters for field capacity, one as a fraction of soil volume and the other as a percent of saturation, are used in the equations for two different processes. Because the equations that they enter into are of different importance, the two parameters are of different sensitivity. Another important soil parameter which controls the connection between soil water content and decomposition is *msat*, which is proportional to the relative rate of decomposition occurring at saturation. This parameter is important for most systems except the Mediterranean shrubland, xeromorphic woodland, and tundras.

The calibration parameters are important in all 17 vegetation types to the total system sensitivity; of these, usually K_d is the most important and K_r, the least. The importance of the calibration parameters suggests that the model results are strongly influenced by estimates of model fluxes and standing crops from which the calibration parameters are derived. The most common ordering in total system sensitivity for the eight calibration parameters is K_d, N_{loss}, K_{fall}, N_{max}, C_{max}, L_{nc}, N_{up}, and K_r, from the most sensitive to the least. This suggests that immobilization and plant respiration are less important on a relative basis for the total system, and soil respiration and nitrogen losses from soils are the most important processes. Deviation from this ordering occurs in some systems. For example, the total system is relatively more sensitive to increased immobilization in wet tundra in which N_{up} ranks third in importance among calibration parameters. This suggest that this system is strongly limited by nitrogen. The relatively strong sensitivity to N_{up} is consistent with wet tundra's relatively strong response to k_{n2}.

Table 14. Net change in terrestrial carbon storage [$\Delta C = \Delta(C_s + C_v)$] (g m^{-2}) for a 10% change in each parameter for systems 1 through 6.

System 1	ΔC	System 2	ΔC	System 3	ΔC	System 4	ΔC	System 5	ΔC	System 6	ΔC
m_{opt}	978	m_{opt}	2455	m_{opt}	771	m_{opt}	6492	m_{opt}	6006	m_{opt}	4524
K_d	-471	K_d	-1075	fc_{sat}	-567	fc_{sat}	-1517	fc_{sat}	-4521	K_d	-940
fc_{sat}	-429	pv_{sv}	966	L_{nc}	-444	$msat$	-1192	fc_{sv}	3329	$msat$	-873
N_{max}	265	L_{nc}	-740	K_d	-421	K_d	-942	N_{max}	2978	Q_{10}	-808
C_{max}	263	C_{max}	650	N_{max}	253	N_{max}	928	C_{max}	2973	pv_{sv}	648
L_{nc}	-260	N_{max}	571	fc_{sv}	242	C_{max}	924	L_{nc}	-2969	T_{opt}	-637
a_{leaf}	240	K_r	-493	C_{max}	239	L_{nc}	-924	T_{min}	2068	fc_{sat}	-577
k_{n1}	-171	k_{n1}	-467	k_{n1}	-229	k_{n1}	-719	K_r	-2042	T_{min}	561
K_r	-164	N_{up}	-433	K_r	-198	N_{loss}	-711	K_{fall}	-2031	N_{max}	521
T_{opt}	-162	T_{opt}	-406	k_{CO2}	-184	K_r	-432	pv_{sv}	-2024	C_{max}	520
N_{loss}	-151	fc_{sat}	-395	c_1	165	k_{CO2}	-431	T_{opt}	-1838	L_{nc}	-508
pv_{sv}	139	T_{min}	334	k_{lgt}	-164	K_{fall}	-412	k_{n1}	-1782	wp_{sv}	-358
T_{min}	131	fc_{sv}	-294	T_{min}	155	Q_{10}	-398	N_{loss}	-1751	k_{n1}	-344
fc_{sv}	130	k_{n2}	277	c_2	145	pv_{sv}	348	K_d	-1636	N_{loss}	-338
c_1	120	c_1	275	K_{fall}	-140	lai_{max}	-321	k_{CO2}	-1250	mst_{mn}	-283
b_{leaf}	113	a_{leaf}	272	r_{grfc}	-139	cn_{max}	-262	Q_{10}	-1164	k_{CO2}	-248
min_{leaf}	110	min_{leaf}	227	k_{lsr}	132	T_{opt}	-256	lai_{max}	-1024	K_r	-208
k_{CO2}	-104	k_{lsr}	220	ahd_t	131	T_{min}	248	$msat$	-878	rt	204
k_{lgt}	-95	k_{CO2}	-219	T_{tcd}	131	S_p	217	S_p	875	K_{fall}	154
ml	90	K_{fall}	211	N_{loss}	-130	k_{lgt}	-215	cn_{max}	-764	ml	-151
c_2	89	c_2	208	s_{td}	130	mst_{mn}	-204	k_{lgt}	-762	T_{max}	121
T_{max}	80	k_{lgt}	-183	ml	128	c_1	201	τ	735	K_{min}	109
Q_{10}	-79	b_{leaf}	161	s_{nt}	126	ml	196	β	596	b_{leaf}	103
K_{fall}	70	T_{max}	149	a_{leaf}	125	τ	194	c_1	555	k_{lgt}	-101
lai_{max}	56	Q_{10}	-147	N_{up}	-124	r_{grfc}	-188	c_2	504	r_{grfc}	-96
c_{leaf}	55	lai_{max}	141	$cldsoil$	122	β	179	cld_1	430	cld_2	79
k_{lsr}	53	N_{loss}	-139	wp_{sv}	-112	c_2	178	cld_2	422	S_p	57

The sensitivity for k_{n2} for wet tundra is 0.23. This is the highest value for k_{n2} for all systems. The parameter k_{n2} is the value of available nitrogen at which immobilization is at half the potential maximum. The strong response of the wet tundra system to both N_{up} and k_{n2} suggest the sensitivity of this system to immobilization. The parameter k_{n1} is the value of available nitrogen ($K_s N_{av}$) at which plant uptake is at half its maximum possible level. The total system sensitivity for this parameter is between 0.23 and 0.32 for systems 1 through 7, 12, 14, and 17. Thus the systems are relatively sensitive to the process of plant uptake of nitrogen. There is more evidence given below that the colder systems of this group are nitrogen limited.

It is interesting to note that Q_{10} is least important for the coldest systems with a total system sensitivity of about 0.13. As the average temperature of the system increases, Q_{10} becomes more important with a total system sensitivity value of about 1.0 in temperate systems and values of 1.3 to 2.0 for tropical systems. The sensitivity of the systems to the parameter controlling the response of gross primary productivity k_{CO2} falls within a narrow range from 0.12 to 0.21.

There were a total of 62 parameters tested for sensitivity. Out of the 17 systems, 11 are insensitive to over 30 parameters; two systems (temperate savanna and short grassland) are insensitive to 20 to 29 parameters; two systems (tall grassland and wet tundra) are insensitive to 10 to 19 parameters; and two system are insensitive (dry tundra and boreal woodland) to less than 10 parameters. The fact that the colder systems are sensitive to more parameters on average does suggest that these systems may be somewhat more fragile

Table 15. Net change in terrestrial carbon storage [$\Delta C=\Delta(C_S+C_V)$] (g m^{-2}) for a 10% change in each parameter for systems 7 through 12.

System 7	ΔC	System 8	ΔC	System 9	ΔC	System 10	ΔC	System 11	ΔC	System 12	ΔC
m_{opt}	2533.4	Q_{10}	-2357	m_{opt}	2343.7	m_{opt}	4355.2	m_{opt}	4557.4	m_{opt}	4369.3
m_{sat}	-493.9	K_d	-1449	K_d	-511.6	fc_{sat}	-1331	fc_{sat}	-1337	fc_{sat}	-1971
pv_{sv}	417.4	fc_{sv}	1077.5	Q_{10}	-406.6	N_{max}	1285.3	N_{max}	1210.0	T_{opt}	-1340
K_d	-337.8	m_{opt}	923.5	pv_{sv}	389.9	C_{max}	1284.8	C_{max}	1209.7	N_{max}	1334.4
Q_{10}	-330.1	C_{max}	794.4	C_{max}	368.9	L_{nc}	-1250	L_{nc}	-1209	C_{max}	1332.8
wp_{sv}	-306.5	N_{max}	791.3	N_{max}	368.9	K_d	-1007	K_d	-976.7	L_{nc}	-1309
fc_{sat}	-217.6	L_{nc}	-790.6	L_{nc}	-367.1	K_{fall}	-901.2	K_{fall}	-776.6	K_d	-1164
C_{max}	196.7	fc_{sat}	-567.9	m_{sat}	-305.7	a_{leaf}	750.6	Q_{10}	-753.8	fc_{sv}	832.8
N_{max}	195.3	K_r	-359.4	fc_{sv}	-305.6	Q_{10}	-576.5	K_r	-637.7	K_{fall}	-786.0
L_{nc}	-188.6	k_{CO2}	-348.0	al_{eaf}	290.0	K_r	-537.7	k_{n1}	-522.2	Q_{10}	-745.9
T_{opt}	-170.8	pv_{sv}	-343.0	fc_{sat}	-263.1	k_{n1}	-490.1	N_{loss}	-498.9	k_{n1}	-731.3
k_{n1}	-130.2	T_{opt}	-325.3	T_{opt}	-212.4	k_{CO2}	-488.3	m_{sat}	-496.1	N_{loss}	-726.6
mst_{mn}	-126.2	K_{fall}	293.8	S_p	176.4	N_{loss}	-471.8	k_{CO2}	-494.2	K_r	-616.4
N_{loss}	-124.9	m_{sat}	-234.5	k_{CO2}	-146.9	m_{sat}	-410.8	T_{min}	387.2	T_{min}	610.0
b_{leaf}	110.0	N_{loss}	-218.0	K_r	-138.4	b_{leaf}	305.6	c_{leaf}	328.8	k_{CO2}	-538.2
T_{min}	90.6	lai_{max}	-216.0	b_{leaf}	133.7	k_{lgt}	-298.3	T_{opt}	-319.5	pv_{sv}	-534.4
k_{CO2}	-88.1	k_{n1}	-213.8	τ	118.8	T_{opt}	-271.7	k_{lgt}	-318.5	S_p	448.2
K_r	-67.3	k_{lgt}	-190.4	β	114.9	S_p	243.0	b_{leaf}	306.8	lai_{max}	-406.0
S_p	64.7	T_{min}	146.6	k_{n1}	-113.7	$rgrfc$	-213.6	al_{eaf}	273.4	k_{lgt}	-377.1
fc_{sv}	-57.1	cn_{max}	-137.0	cn_{max}	110.7	τ	183.6	lai_{max}	-242.5	τ	365.6
τ	45.9	$rgrfc$	-125.4	N_{loss}	-109.0	β	163.0	S_p	241.9	m_{sat}	-345.6
K_{min}	43.0	pl	119.7	lai_{max}	105.6	fc_{sv}	161.9	cn_{max}	-193.1	β	308.3
β	42.0	$cld2$	119.0	$c2$	104.3	$cld2$	158.7	$rgrfc$	-189.6	$c1$	284.2
rt	41.7	k_{can}	-104.9	T_{min}	93.0	T_{min}	156.3	τ	175.7	$c2$	261.2
cn_{max}	41.2	b_{leaf}	89.4	k_{lgt}	-89.6	$cld1$	154.5	β	158.1	$cld1$	240.6
k_{lgt}	-41.1	wp_{sv}	83.5	ml	-89.6	$c2$	144.3	$cld1$	138.2	T_{max}	229.0
K_{fall}	40.4	$cld1$	72.8	$c1$	85.9	$c1$	140.3	$c2$	133.7	$rgrfc$	-195.6

than their neighbors in more temperate climates. Usually the insensitive parameters are related to the detailed functioning of the water balance model.

Two parameters from the water balance model that are usually sensitive are lai_{max} (maximum leaf area index) and cn_{max} (maximum stomatal conductance). These two parameters are usually listed in the rankings near each other and they both enter into the process of transpiration in the water balance model. The sensitivity of the model to these two parameters has a correlation coefficient of 0.98.

Sensitivity of stored carbon at steady state to changes in model parameters.–In Tables 14, 15, and 16, we show the net change in terrestrial stored carbon ΔC at steady state for a 10% increase in each parameter for the 27 parameters producing the largest changes in systems 1 through 6, 7 through 12, and 13 through 17, respectively. The net change in stored carbon ΔC is given by

$$\Delta C_k = C_v\left(p_{j,nominal}\Big|_{j\neq k}, p_{k,new}\right) + C_s\left(p_{j,nominal}\Big|_{j\neq k}, p_{k,new}\right) - C_v\left(p_{j,nominal}\right) - C_s\left(p_{j,nominal}\right) \tag{17}$$

$$= \Delta C_{v,k} + \Delta C_{s,k}$$

Table 16. Net change in terrestrial carbon storage [$\Delta C = \Delta(C_s + C_v)$] (g m^{-2}) for a 10% change in each parameter for systems 13 through 17.

System 13	ΔC	System 14	ΔC	System 15	ΔC	System 16	ΔC	System 17	ΔC
Q_{10}	-2234.7	m_{opt}	3336.7	Q_{10}	-2241.1	m_{opt}	3586.9	fc_{sat}	-2715.3
m_{opt}	1604.3	Q_{10}	-1081.1	K_d	-1053.0	Q_{10}	-1475.2	Q_{10}	-2472.4
K_d	-1047.3	$msat$	-785.6	L_{nc}	-770.1	L_{nc}	-924.6	fc_{sv}	2414.0
L_{nc}	-766.6	K_d	-714.7	N_{max}	751.0	N_{max}	905.0	pv_{sv}	-2377.4
C_{max}	753.3	L_{nc}	-451.3	C_{max}	750.0	C_{max}	904.9	L_{nc}	-1796.0
N_{max}	750.7	fc_{sat}	-446.8	fc_{sv}	681.4	K_d	-740.8	N_{max}	1773.9
b_{leaf}	690.5	N_{max}	445.3	m_{opt}	592.4	fc_{sat}	-617.7	C_{max}	1772.8
fc_{sat}	-483.3	C_{max}	445.3	K_r	-456.1	$msat$	-603.3	K_d	-1355.3
K_r	-450.9	T_{opt}	-413.8	fc_{sat}	-455.0	K_r	-590.3	m_{opt}	1102.6
pv_{sv}	346.3	mst_{mn}	-369.4	k_{CO2}	-300.6	b_{leaf}	538.9	K_r	-1074.1
k_{CO2}	-334.9	k_{n1}	-326.1	pv_{sv}	-241.8	pv_{sv}	478.0	K_{fall}	-1072.5
S_p	-247.9	N_{loss}	-315.2	kl_{gt}	-179.1	K_{fall}	-469.6	N_{loss}	-1068.7
cn_{max}	-230.3	ml	-307.5	k_{n1}	-167.0	k_{CO2}	-410.2	k_{n1}	-1065.7
lai_{max}	-223.7	wp_{sv}	-273.7	N_{loss}	-166.5	k_{n1}	-309.9	wp_{sv}	795.4
a_{leaf}	207.5	pv_{sv}	270.3	r_{grfc}	-162.1	N_{loss}	-298.7	k_{CO2}	-768.8
r_{grfc}	-187.0	b_{leaf}	237.3	wp_{sv}	151.6	a_{leaf}	295.8	T_{opt}	-460.2
k_{n1}	-182.1	K_r	-226.9	cn_{max}	-134.9	wp_{sv}	-272.6	kl_{gt}	-450.5
N_{loss}	-181.8	K_{min}	139.7	b_{leaf}	133.6	kl_{gt}	-229.9	lai_{max}	-424.6
kl_{gt}	-174.6	k_{CO2}	-136.4	lai_{max}	-131.1	T_{opt}	-198.0	b_{leaf}	416.2
τ	-168.1	kl_{gt}	-97.0	$msat$	-102.8	S_p	164.2	a_{leaf}	411.1
c_{leaf}	-159.3	K_{fall}	87.6	cld_2	87.9	mst_{mn}	-147.0	cn_{max}	-307.0
β	-152.9	T_{min}	87.5	cld_1	73.9	c_{leaf}	136.0	cld_1	262.0
c_2	-140.2	lai_{max}	-86.7	r_a	-63.6	cld_2	122.1	$msat$	-234.9
fc_{sv}	126.5	r_{grfc}	-68.4	p_l	61.8	r_{grfc}	-117.1	r_{grfc}	-205.1
k_{can}	-123.8	cld_2	55.6	k_{can}	52.5	β	102.1	cld_2	177.9
r_a	-120.3	T_{max}	54.5	c_{leaf}	43.8	τ	100.5	c_{leaf}	167.5
p_l	111.9	cn_{max}	-43.5	rt		cld_1	98.6	rt	147.5

where $\{p_{j,nominal}\}$ is the set of model parameters with nominal values, $\left\{p_{j,inominal}, p_{k,new}\right\}_{j \neq k}$ is the set of nominal parameters except for the kth parameter which is 10% larger than nominal, $\Delta C_{v,k}$ is the change in carbon stored in vegetation, and $\Delta C_{s,k}$ is the change in carbon stored in the soil.

　　We see that an increase in the parameter m_{opt}, the soil moisture at which decomposition respiration is optimum, produces a substantial increase in stored carbon for all systems. Increasing m_{opt} produces a decrease in soil respiration. Likewise, an increase in the respiration parameter K_d results in a large decrease in stored soil carbon for all systems. In fact, all the calibration parameters except for N_{up} (with low importance in 15 systems) and K_{fall} (with low importance in 5 systems) are very important in determining stored carbon. As might be expected increasing C_{max}, the intrinsic rate of gross primary productivity, increases carbon stored by the vegetation and soils; increasing the intrinsic rate of nitrogen uptake by plants N_{max} also leads to more stored carbon; and an increase in plant respiration rate K_r causes a decrease in net primary production and the total stored carbon in the system. Note that a 10% increase in C_{max} and N_{max} both produces almost exactly same change in stored carbon. Likewise the absolute value of the change in stored carbon resulting from an increase in L_{nc} (the parameter controlling the transfer of nitrogen from vegetation to soil due to litterfall) is similar to the changes produced by C_{max} and

N_{max}. Increasing nitrogen loss from vegetation by increasing L_{nc} decreases carbon in

Table 17. Change in net primary productivity (δNPP gC m^{-2}yr^{-1}) for a 10% change in the model parameter for vegetation types 1 through 6.

System 1	δNPP	System 2	δNPP	System 3	δNPP	System 4	δNPP	System 5	δNPP	System 6	δNPP
fc_{sv}	5.0	m_{opt}	-11.3	pv_{sv}	-12.2	pv_{sv}	-17.6	fc_{sv}	41.5	T_{opt}	-6.3
fc_{sat}	-4.4	fc_{sv}	5.4	fc_{sat}	-11.9	fc_{sat}	-16.7	fc_{sat}	-38.9	pv_{sv}	-6.0
pv_{sv}	-4.3	pv_{sv}	-5.1	fc_{sv}	11.6	m_{opt}	-14.7	pv_{sv}	-38.3	fc_{sat}	-5.7
m_{opt}	-4.2	L_{nc}	-4.7	m_{opt}	-10.4	wp_{sv}	11.9	N_{max}	25.5	T_{min}	5.5
L_{nc}	-2.7	C_{max}	4.2	L_{nc}	-9.3	N_{max}	10.3	C_{max}	25.4	N_{max}	5.1
N_{max}	2.6	K_d	3.9	N_{max}	5.2	C_{max}	10.2	L_{nc}	-25.4	C_{max}	5.1
C_{max}	2.6	N_{max}	3.7	k_{n1}	-4.9	L_{nc}	-10.1	K_r	-17.6	L_{nc}	-5.1
a_{leaf}	2.3	K_r	-3.1	C_{max}	4.9	k_{n1}	-7.9	T_{min}	17.6	lai_{max}	-3.7
k_{n1}	-1.8	k_{n1}	-3.0	K_r	-4.1	N_{loss}	-7.8	K_{fall}	17.5	k_{n1}	-3.4
K_r	-1.7	N_{up}	-2.7	k_{CO2}	-3.8	lai_{max}	-7.5	T_{opt}	-15.9	N_{loss}	-3.3
T_{opt}	-1.7	T_{opt}	-2.6	Q_{10}	3.5	cn_{max}	-6.9	k_{n1}	-15.4	Q_{10}	2.9
N_{loss}	-1.6	fc_{sat}	-2.6	k_{lgt}	-3.4	fc_{sv}	6.2	N_{loss}	-15.2	cn_{max}	-2.7
T_{min}	1.4	K_{fall}	1.8	c_1	3.3	K_r	-4.7	lai_{max}	-13.4	wp_{sv}	2.4
k_{CO2}	-1.1	k_{n2}	1.8	T_{min}	3.2	k_{CO2}	-4.7	cn_{max}	-11.1	k_{CO2}	-2.4
c_1	1.1	a_{leaf}	1.7	r_{grfc}	-3.0	Q_{10}	4.7	k_{CO2}	-10.8	m_{opt}	-2.2
K_{fall}	1.1	Q_{10}	1.7	c_2	2.9	K_{fall}	4.7	S_p	6.7	K_r	-2.0
b_{leaf}	1.1	c_1	1.5	N_{loss}	-2.8	$cldsoil$	3.9	k_{lgt}	-6.6	K_{fall}	2.0
min_{leaf}	1.0			T_{tcd}	2.7	ml	3.0	τ	5.7	k_{can}	-1.4
k_{lgt}	-0.9	k_{CO2}	-1.5	ahd_t	2.7	T_{opt}	-2.8	rt	5.6	p_l	1.4
ml	0.9	min_{leaf}	1.4	s_{td}	2.6	T_{min}	2.7	Q_{10}	4.8	fc_{sv}	1.3
Q_{10}	0.8	k_{lsr}	1.4	K_d	2.6	k_{lgt}	-2.6	β	4.6	T_{max}	1.2
c_2	0.8	k_{lgt}	-1.3	N_{up}	-2.6	r_{grfc}	-2.6	c_1	4.3	S_p	-1.2
T_{max}	0.8	c_2	0.8	k_{lsr}	1.1	K_{min}	2.6	c_2	3.9	K_{min}	1.1
K_d	0.8	$msat$	0.9	ml	1.0	c_1	2.6	cld_1	3.7	k_{lgt}	-1.0
r_{grfc}	-0.7	b_{leaf}	0.9	s_{nt}	0.9	c_2	2.6	cld_2	3.6	r_{grfc}	-0.9
$msat$	0.5	T_{max}	0.9	$msat$	0.9	ahd_t	2.5	T_{max}	3.2	cld_2	0.8
c_{leaf}	0.5	N_{loss}	-0.9	a_{leaf}	-0.9	α	-1.3	α	3.0	b_{leaf}	0.7

vegetation thereby reducing gross primary productivity because the allocation parameter ac is reduced as the C:N ratio increases.

We note that Q_{10} is of relatively low importance for cold climate systems, of moderate importance for temperate systems, and of high importance in tropical systems in controlling carbon storage. This result comes from the relative temperature in these systems. Increasing Q_{10} increases respiration form both vegetation and soil. The parameter T_{opt} is of moderate to high importance for carbon storage in all systems except boreal woodland, Mediterranean shrubland, and xeromorphic woodland. Note that for the rest of the systems increasing T_{opt} lowers carbon storage. This suggests that the 14 systems in which T_{opt} is important have temperatures well below the optimum for much of the growing season. Note that in forested systems (high levels of carbon in vegetation) increasing K_{fall} reduces carbon storage, but in shrubland, grassland, tundra, and tropical savanna (low carbon content in vegetation, high carbon content in soil) increasing K_{fall} increases carbon storage. Increasing the nitrogen loss rate from the soil and the system (N_{loss}) lowers productivity and carbon storage in all systems

Increasing light (i.e., increasing S_p, τ, β, c_1, c_2, cld_1, and cld_2) in some systems (boreal forest, all four temperate forests, and temperate savanna) produce substantial increases in carbon storage. Increasing these parameters in other systems that are not light-limited produces little or no change. In a third class for which radiation is a source of water stress (i.e., Mediterranean shrubland) increasing these parameters produces a reduction in carbon storage.

Table 18. Change in net primary productivity (δNPP gC m^{-2} yr^{-1}) for a 10% change in the model parameter for vegetation types 7 through 12.

System 7	δNPP	System 8	δNPP	System 9	δNPP	System 10	δNPP	System 11	δNPP	System 12	δNPP
pv_{sv}	-11.2	C_{max}	20.3	L_{nc}	-21.2	fc_{sv}	32.8	fc_{sv}	35.1	fc_{sv}	60.7
fc_{sat}	-10.6	L_{nc}	-20.2	N_{max}	21.2	pv_{sv}	21.2	fc_{sat}	-34.2	pv_{sv}	-60.5
wp_{sv}	9.6	N_{max}	20.2	C_{max}	20.2	fc_{sat}	21.2	pv_{sv}	-34.0	fc_{sat}	-59.7
C_{max}	9.6	Q_{10}	18.1	Q_{10}	16.1	N_{max}	16.1	L_{nc}	-30.9	T_{opt}	-40.6
N_{max}	9.5	fc_{sat}	-14.5	pv_{sv}	-15.7	C_{max}	-15.7	N_{max}	30.8	N_{max}	40.4
L_{nc}	-9.2	pv_{sv}	-14.1	fc_{sat}	-15.3	L_{nc}	-15.3	C_{max}	30.8	C_{max}	40.3
T_{opt}	-8.3	fc_{sv}	11.3	fc_{sv}	14.7	Q_{10}	14.7	lai_{max}	-24.6	L_{nc}	-39.6
Q_{10}	7.9	K_r	-9.2	lai_{max}	-12.5	a_{leaf}	-12.5	cn_{max}	-22.4	lai_{max}	-28.6
k_{n1}	-6.3	K_{fall}	9.0	T_{opt}	-12.3	K_r	-12.3	Q_{10}	16.5	Q_{10}	24.0
N_{loss}	-6.1	k_{CO2}	-8.9	cn_{max}	-8.9	K_{fall}	-11.3	K_r	-16.3	k_{n1}	-22.2
lai_{max}	-5.1	T_{opt}	-8.3	k_{CO2}	-8.3	lai_{max}	-8.6	K_{fall}	15.3	N_{loss}	-22.0
T_{min}	4.4	$Nloss$	-5.6	K_r	-5.6	k_{n1}	-8.1	k_{n1}	-13.4	cn_{max}	-21.8
k_{CO2}	-4.3	k_{n1}	-5.5	K_{fall}	-5.5	k_{CO2}	7.6	N_{loss}	-12.8	K_r	-18.7
cn_{max}	-3.9	lai_{max}	-5.1	k_{n1}	-5.1	cn_{max}	-6.6	k_{CO2}	-12.7	T_{min}	18.4
pl	3.4	k_{lgt}	-4.9	N_{loss}	-4.9	N_{loss}	-6.4	T_{min}	9.8	K_{fall}	18.3
K_{fall}	3.4	T_{min}	3.7	S_p	3.7	k_{lgt}	-6.1	T_{opt}	-8.2	k_{CO2}	-16.3
K_r	-3.3	cn_{max}	-3.3	T_{min}	-3.3	T_{opt}	5.3	k_{lgt}	-8.1	k_{lgt}	-11.4
k_{can}	-3.0	r_{grfc}	-3.2	k_{lgt}	-3.2	b_{leaf}	-5.2	rt	5.0	cld_1	7.3
m_{opt}	-2.4	cld_2	3.0	a_{leaf}	3.0	r_{grfc}	5.0	r_{grfc}	-4.9	d_{cE}	-6.9
K_{min}	2.1	wp_{sv}	2.9	k_{can}	2.9	rt	-4.5	b_{leaf}	3.6	T_{max}	6.9
fc_{sv}	2.0	pl	2.7	r_{grfc}	2.7	cld_2	-4.1	cld_1	3.5	τ	6.8
k_{lgt}	-2.0	b_{leaf}	2.4	β	2.4	T_{min}	-3.8	ahd_t	-3.5	S_p	6.4
S_p	-2.0	k_{can}	-2.4	pl	-2.4	cld_1	3.8	c_{leaf}	3.4	rt	6.1
r_{grfc}	-1.8	cld_1	1.8	c_2	1.8	$al(su)$	-3.6	cld_2	3.1	r_{grfc}	-5.9
T_{max}	1.4	T_{max}	1.1	τ	1.1	c_{leaf}	-3.3	d_{cE}	-2.5	cld_2	5.5
cld_2	1.3	rt	1.1	b_{leaf}	1.1	pl	2.7	s_{ahd}	2.5	c_1	5.0
β	-1.2	$al(su)$	1.0	cld_2	1.0	d_{cE}	2.6	a_{leaf}	2.2	β	4.9

Immobilization parameters (N_{up} and k_{n2}) appear to be relatively unimportant for most systems. However the parameters for plant uptake of nitrogen (N_{max} and k_{n1}) are quite important. Both parameters usually produce a marked change in carbon storage.

Rooting depth is of moderate to low importance in tropical forests, arid shrubland, short grassland, and xeromorphic woodland. In the rest of these systems it is of only minor importance.

Sensitivity of net primary production at steady state to changes in model parameters.–We show the changes in annual net primary productivity for a 10% increase in the 27 most important parameters for systems 1 through 6, 7 through 12, and 13 through 17, in Tables 17, 18, and 19, respectively. Changes in the two parameters fc_{sat} and pv_{sv} both produce about the same strong effect on productivity for all systems. They both enter into eq. A.87 to produce a reduction in the availability of inorganic nitrogen and a reduction in nitrogen uptake; fc_{sat} enters directly and pv_{sv} enters by its incorporation into M (eq. A.79). This reduction in nitrogen uptake results in a loss of productivity. When ecosystems are not particularly water-limited, changes in fc_{sv} produce a positive effect on productivity with the same magnitude as changes in fc_{sat}. That is, in the non-water-limited systems: temperate coniferous forest site (system 5), the two tundras (systems 1 and 2), boreal woodland (system 3), tall grassland, temperate savannas, and temperate forests (systems 8 through 12), if fc_{sv} increases, then M increases relative to fc_{sat} in eq. A.87 producing an increase in nitrogen availability and an increase in productivity. In the other, water-limited systems the effect of increasing fc_{sv} is to produce a higher potential water

Table 19. Change in net primary productivity (δNPP gC m^{-2}yr^{-1}) for a 10% change in the model parameter for vegetation types 13 through 17.

System 13	δNPP	System 14	δNPP	System 15	δNPP	System 16	δNPP	System 17	δNPP
L_{nc}	-26.5	pv_{sv}	-21.4	L_{nc}	-26.5	L_{nc}	-34.0	fc_{sat}	-76.1
C_{max}	25.9	wp_{sv}	20.9	N_{max}	25.9	N_{max}	33.3	pv_{sv}	-72.3
N_{max}	25.8	L_{nc}	-20.9	C_{max}	25.9	C_{max}	33.3	L_{nc}	-50.3
b_{leaf}	23.0	fc_{sat}	-20.7	K_r	-15.7	fc_{sat}	-22.7	fc_{sv}	50.0
pv_{sv}	-17.7	N_{max}	20.5	fc_{sat}	-15.7	pv_{sv}	-21.8	N_{max}	49.6
fc_{sat}	-16.7	C_{max}	20.5	pv_{sv}	-15.4	K_r	-21.7	C_{max}	49.6
K_r	-15.6	T_{opt}	-19.2	Q_{10}	14.5	fc_{sv}	21.5	K_r	-30.1
Q_{10}	14.6	Q_{10}	15.9	K_{fall}	14.3	K_{fall}	21.2	N_{loss}	-30.0
K_{fall}	14.0	k_{n1}	-15.1	fc_{sv}	11.8	b_{leaf}	15.8	k_{n1}	-29.9
k_{CO2}	-11.6	N_{loss}	-14.6	k_{CO2}	-10.3	k_{CO2}	-15.1	K_{fall}	28.8
cn_{max}	-7.1	K_r	-10.6	k_{lgt}	-6.2	k_{n1}	-11.3	Q_{10}	28.3
a_{leaf}	6.9	K_{fall}	10.2	N_{loss}	-5.8	N_{loss}	-11.0	wp_{sv}	24.4
lai_{max}	-6.8	b_{leaf}	9.1	k_{n1}	-5.7	Q_{10}	10.6	k_{CO2}	-21.6
S_p	-6.8	lai_{max}	-7.4	r_{grfc}	-5.5	a_{leaf}	8.7	T_{opt}	-13.0
r_{grfc}	-6.4	K_{min}	6.4	cn_{max}	-4.6	k_{lgt}	-8.4	k_{lgt}	-12.7
k_{n1}	-6.3	k_{CO2}	-6.3	b_{leaf}	4.5	lai_{max}	-7.2	lai_{max}	-11.7
m_{opt}	-6.3	cn_{max}	-5.5	lai_{max}	-4.4	b_{leaf}	7.0	b_{leaf}	11.6
wp_{sv}	6.3	k_{lgt}	-4.6	wp_{sv}	-4.4	a_{leaf}	-6.7	a_{leaf}	11.4
N_{loss}	-6.3	T_{min}	3.9	cld_2	3.3	cn_{max}	5.7	cn_{max}	-8.5
k_{lgt}	-6.1	S_p	-3.2	cld_1	3.0	cld_1	-5.1	cld_1	7.3
c_{leaf}	-5.4	r_{grfc}	-3.2	ra	-2.1	cld_2	4.5	r_{grfc}	-5.8
τ	-4.6	p_l	3.0	p_l	2.1	r_{grfc}	-4.3	cld_2	4.9
β	-4.1	k_{can}	-2.7	k_{can}	-1.8	c_{leaf}	4.2	m_{opt}	4.6
fc_{sv}	3.9	fc_{sv}	2.5	c_{leaf}	1.8	cld_1	3.7	c_{leaf}	4.6
k_{can}	-3.7	cld_2	2.5	rt	1.6	m_{opt}	2.7	rt	4.1
ra	-3.7	T_{max}	2.4	d_{cE}	-1.1	K_{min}	2.6	c_{ip}	-2.6
c_2	-3.7	cld_1	1.8	m_{opt}	-1.1	p_l	2.5	K_{min}	1.6

reservoir to fill in the soil. Since precipitation is limited in these systems, this larger reservoir produces a relatively drier soil and productivity is reduced.

Increasing the nitrogen uptake rate (N_{max}) or carbon assimilation rate (C_{max}) by the same percentage usually produces almost exactly the same substantial increase in productivity. Increasing the nitrogen loss rate from vegetation (L_{nc}) produces a corresponding drop in productivity. Of usually less importance, increasing the net loss from the system as a whole (N_{loss}) produces a net loss in productivity. Productivity is insensitive to the parameters for soil respiration rate K_d (except in the tundras and boreal woodland) and nitrogen immobilization N_{up}. Increasing K_{fall} acts to decrease carbon relative to nitrogen in vegetation because the carbon removed by litterfall is respired, but the nitrogen removed by litterfall is recycled. The system responds with an increase in ac (eq. A.99) which produces greater productivity. Thus increasing K_{fall} produces a moderately important stimulative effect on productivity. Increasing K_r increases respiration and reduces net primary production by definition, eq. A.83 and eq. 14. Likewise increasing growth respiration by increasing r_{grfc} also reduces npp for all systems.

Depending on the relation of ambient temperature to T_{opt}, T_{max}, and T_{min}, changes in these parameters can have a substantial effect on productivity or very little effect. Usually the typical average daily temperature is below T_{opt} and so increasing T_{opt} results in a substantial decrease in productivity. Recall that T_{min} or T_{max} are changed by increasing the half-distance between T_{min} and T_{max} by 10% and then adding (or subtracting) the increased half-distance to (or from) the average of T_{min} and T_{max} to produce the new T_{max}

(or T_{min}). The equation for gross primary productivity as a function of temperature (eq. A.75) is such that either increasing T_{max} or decreasing T_{min} increases *gpp* for any temperature between the two limits except the optimum which is fixed at 1. Thus lowering T_{min} or raising T_{max} produces an increase in net primary productivity. Usually the change in T_{max} results in an insignificant increase in productivity, but the change in T_{min} results in a moderate increase.

Increasing Q_{10} always increases net primary productivity. On a relative basis, this effect is strongest in the temperate systems and weakest in the tropics and high latitudes. The effect of increasing $Q10$ producing an increase in *npp* arises through accelerated nitrogen cycling even though increasing Q_{10} increases plant respiration which would otherwise decrease *npp*.

We see that net primary productivity is at least slightly light-limited in all systems in that increasing k_{lgt} reduces productivity by a small to moderate amount. Recall that k_{lgt} is the light level at which the Michaelis-Menten expression for gross primary productivity response to light is at half its maximum. The temperate coniferous forest site in particular is light limited with little or no water limitation. This system shows a positive response in *npp* to all parameters whose increase produces an increase in light level, i.e., α, β, τ, c_1, c_2, cld_1, cld_2, and S_p. The arid shrubland, on the other hand, only shows a positive response to k_{lgt}. In fact, increasing S_p in the arid shrubland reduces productivity because even though light increases, the resulting water stress from higher radiation causes a net reduction in transpiration and conductivity.

Another parameter whose increase shows a ubiquitous, moderate reduction in productivity across all systems is k_{n1}. This parameter is the value of available nitrogen at which the Michaelis-Menten expression for plant uptake is at half maximum. Increasing k_{n1} reduces nitrogen uptake which results in a reduction in gross primary production through the response of the variable *ac*. For systems 4 through 17, an increase in lai_{max} shows a substantial to moderate reduction in productivity. Note that C_{max} implicitly contains the maximum leaf area index. Thus changing lai_{max} does not change *gpp* directly. The parameter lai_{max}, as used in the model, only affects the water balance portion of the model. Increasing lai_{max} increases light absorption in the canopy, transpiration, interception, evaporation, and water stress. It is this mechanism that results in the loss of productivity. In the tall grassland, temperate forests, xeromorphic woodland, and tropical forests, increasing the rooting depth *rt* results in a moderate increase in productivity. In these systems, there is either substantial amounts of precipitation or water-conserving properties such that more soil water can be retained by deeper soils.

Increasing the parameter k_{CO2} also reduces *npp* across all systems. This parameter is found in eq. A.74 and is the level of internal CO_2 at which *gpp* is at half maximum. Increasing this parameter reduces *gpp* for fixed internal CO_2 C_i. Because of the direct connection to *gpp*, its effect does not depend on idiosyncrasies of the environment or properties of a particular site.

Unlike the total system sensitivity and total carbon storage, net primary productivity is usually not very sensitive to changes in m_{opt}, the optimum soil moisture for decomposition. Only the nitrogen-limited tundras and boreal systems show a strong response to decreasing soil decomposition by changing the optimum soil water content. In the deciduous systems, increasing either a_{leaf} or b_{leaf} results in larger values of k_{leaf} during the growing seasons and increased gross and net primary production. This effect, while positive, is usually quite modest.

Response of the model to changes in climate and environment

Changes in stored carbon from changes in climate and environment.–In Table 20, we show the net change in total carbon storage in vegetation and soils for changes in environment and climate. If we increase nitrogen input N_{input} to the system by 10%, we see a substantial fertilization effect on stored carbon. In absolute terms, this is particularly

Table 21. Changes in net primary production for changes in driving variables.

System Number	Nominal NPP	Response of NPP to N_{input} e_{NPP} $(10^2$ gC gN$^{-1})$	δNPP (gC m^{-2} yr^{-1})									
			N_{input} + 10%	$T+1$°C	$T+2$°C	Dewpt + 1°C	Sun hr + 10%	Precip. + 10%	CO$_2$ + 10%	2xCO$_2$	2xCO$_2$ $T+1$°C	2xCO$_2$ $T+2$°C
1	65	4.0	2.0	3.5	7.2	0.0	0.2	0.4	1.1	6.4	10.3	14.8
2	120	3.4	1.7	7.2	11.5	0.3	0.2	0.0	1.3	9.1	17.0	23.1
3	170	21.7	5.0	9.2	16.9	0.1	0.6	0.1	2.9	16.8	27.5	37.7
4	220	4.2	8.3	-4.2	-7.5	9.4	0.3	11.0	5.1	31.5	30.9	31.6
5	535	3.1	15.1	6.6	9.4	9.3	2.0	6.6	10.8	66.0	78.6	87.9
6	110	0.7	3.5	2.7	5.2	0.9	-1.0	2.4	2.5	15.8	19.6	23.4
7	200	1.2	6.9	4.2	8.0	2.6	-0.9	10.8	5.1	27.2	33.2	39.5
8	425	0.6	6.2	7.7	13.2	4.0	-0.8	6.6	9.5	53.0	64.8	75.5
9	450	1.2	6.2	3.9	7.6	7.9	-4.6	12.9	8.3	49.1	56.5	64.6
10	650	1.9	11.4	6.0	8.9	8.8	-2.2	11.8	11.5	69.5	79.7	87.5
11	650	2.0	12.1	-4.0	-14.0	14.2	-1.1	15.7	11.8	71.1	69.7	62.8
12	850	4.4	21.9	-8.9	-24.6	25.1	1.4	22.7	16.2	98.3	87.5	71.3
13	550	3.4	6.4	-6.5	-14.8	4.5	-5.7	15.4	11.6	70.5	71.6	70.5
14	435	2.1	14.9	6.0	11.0	3.8	-2.5	20.2	6.1	40.1	52.1	63.8
15	550	3.0	5.7	-2.5	-8.4	4.5	-1.2	9.8	10.2	60.8	64.4	64.3
16	700	0.7	10.4	-18.1	-43.7	4.2	-2.3	15.6	14.5	90.3	78.7	58.9
17	1050	1.5	29.0	7.5	-2.7	10.8	-2.0	16.7	20.6	125.3	145.4	148.1

true in the temperate coniferous forest and tropical evergreen forests, which have high levels of carbon storage under existing nominal conditions. Carbon storage in some systems have particularly low response to nitrogen fertilization. Mediterranean shrubland and xeromorphic woodland show a low response in absolute terms and in relative terms. These two systems had the smallest percent increase of all 17 systems. However, a different statistic is shown in the column in which we give the ratio of the increase in stored carbon to the increase in N_{input}, e_{CN}(gC gN^{-1} yr^{-1})

$$e_{CN} = \frac{\Delta C}{\Delta N_{input}} \tag{18}$$

We see that the two tundra systems, boreal woodland system, and temperate coniferous systems have high values of this statistic. These systems are nitrogen limited. The boreal forest and the temperate broad-leaved evergreen forest come next in response to increased nitrogen inputs. The carbon storage pools of Mediterranean shrubland, xeromorphic forest, arid shrubland, temperate deciduous forest, and temperate mixed forest are of intermediate sensitivity to increased nitrogen. Low values of e_{CN} are found for tropical forests, grasslands, and savannas. Thus the fertilization effect per gram of applied nitrogen should be the greatest at high latitudes, followed by the temperate forests. The tropics and grasslands should have the smallest response.

For a 1°C temperature increase most systems experience a net loss in carbon. The effect of temperature increase on soil respiration and plant respiration outweighs any increase in gross primary productivity for most systems for a 1°C increase. The wet tundra, boreal woodland, temperate coniferous forest, and short grassland are exceptions. The cold systems can experience a sharp increase in *gpp* over a substantial period of time that will compensate for the rise in respiration caused by the increased temperature of 1°C. However, a rise of 2°C is enough to force even the coldest system into a net loss of stored carbon.

Raising the dewpoint lowers the vapor pressure deficit and increases carbon storage for all systems except the tundras and boreal woodland. In these systems, evaporative demand is not a limiting factor and carbon storage is slightly decreased or there is no appreciable change with a 1°C increase in dewpoint.

Increasing hours of sunshine has two effects. More light can produce a positive effect on *gpp*. The resulting increase in production can be especially strong in light-limited systems. However, increasing hours of sunshine also increases net radiation resulting in increased transpiration. In water stressed systems, the increase in transpiration can increase water stress, decrease production and decrease carbon storage. Also, soil water content affects soil decomposition rates. These competing effects can combine to produce effects difficult to predict *a priori* with just a conceptual model. However, as a general rule, the results of TERRA suggest that high latitude and temperate systems show a net positive response to an increase in sunshine hours while low latitude systems show a reduction in carbon storage with increased sunshine.

Increases in precipitation usually result in an increase in production and carbon storage. However in a few systems, wet tundra, arid shrubland, short grassland, and temperate savanna, increased precipitation and soil water content causes an increase in soil respiration that outweighs any increase in productivity.

Doubling CO_2 leads to about a 12 to 14% increase in carbon storage for most systems. The cold-limited systems of the tundras and boreal woodland experience a smaller increase of 8 to 10%. For systems 8 through 17 increasing temperature by 2°C simultaneously with doubling CO_2 produces a drop in carbon storage from the peak attained with just CO_2 doubling alone. This drop in storage is approximately equal to that obtained previously with the 2°C temperature increase alone with no CO_2 doubling. However for systems 2, 3, and 5 through 7, increasing temperature by 2°C in conjunction

with CO_2 doubling produces an increase in carbon storage above that found by just doubling CO_2 with no temperature change. We suggest that this enhanced carbon storage occurs in these systems due to an increase in the soil nitrogen release rate caused by an increase in soil respiration with temperature. This added soil nitrogen, together with the added CO_2, leads to an increase in productivity and an increase in carbon storage. The discussions below on net primary productivity and the transient response of the model emphasize this point.

*Changes in net primary productivity from changes in climate and environment*t.–In Table 21, we show the changes in net primary production resulting from changes in climate and environment. In general, changes in *npp* resulting from increasing nitrogen deposition correlate well with nominal *npp* levels. To see more clearly the relative response of *npp*, we show the efficiency of *npp* response to nitrogen fertilization e_{NPP} (gC gN^{-1}) defined as

$$e_{NPP} = \frac{\delta npp}{\Delta N_{input}} \tag{19}$$

This is the net change in carbon fixed by vegetation (gC m^{-2} yr^{-1}) as a ratio to the change in nitrogen input (N_{input}) (gN m^{-2} yr^{-1}). We see that on this basis boreal woodland is the most responsive system followed by temperate broad-leaved evergreen forest, boreal forest, the two tundra systems, Mediterranean shrubland, and xeromorphic forest. The balance of the temperate and tropical systems are of much lower responsiveness to nitrogen inputs.

Raising temperature has four sources of potential effects of *npp*. First, *gpp* has a positive (negative) response for temperatures below (above) the optimum T_{opt}. Second, plant respiration increases for rising temperatures thereby reducing *npp*. Third, increasing temperature, in the absence of any other changes, can increase the vapor pressure deficit which affects transpiration directly and also affects stomatal conductance thus affecting transpiration indirectly. Changes in transpiration rates can change soil water content. Finally, increasing soil temperature results in an increased rate of soil decomposition which releases nitrogen at a faster than nominal rate. This extra available nitrogen can have a fertilization effect on *npp*. Note that McGuire et al. (1992, 1993) have also reported that increasing temperature in the TEM model increases nitrogen availability because of increased soil respiration and nitrogen mineralization rates. We see that for a 1° and 2°C increase these factors combine for most high latitude and temperate systems to produce a net gain in *npp* at steady state. Most low latitude systems show a net decrease in *npp* as temperature rises. We see that the sign of the change in *npp*, for both the 1°C and 2°C temperature increase, stays the same for all systems except the tropical evergreen forest. In the rest of the systems, the amplitude of the response increases for the 1°C change to the 2°C change. In the tropical evergreen forest, the increase in plant respiration exceeds the other processes as the temperature changes from a 1°C increase to a 2°C increase.

In the high latitude systems, increasing the dewpoint by 1°C produces virtually no changes in *npp*. However, for temperate and tropical systems this increase reduces transpiration, decreases water stress, and increases *npp*. Increasing sunny hours in the high latitude and temperate systems increases *npp*. In the tropics, increasing sunny hours increases net radiation and water stress and decreases *npp*. Increasing precipitation at the high latitudes produces little or no increase in *npp*. However, in the temperate and tropical systems increasing precipitation increases *npp*.

Increasing CO_2 increases *npp* in all systems and usually proportionally to the nominal level of *npp*. A notable exception is the tropical savanna site in which C$_4$ grasses in combination with C$_3$ shrubs and trees shows a smaller gain in *npp* for increased CO_2. In some systems increasing temperature in conjunction with doubling CO_2 produces an

increase in production because of the response of *gpp* to temperature and the increased availability of soil nitrogen. In other systems (e.g., tropical deciduous forest site) the
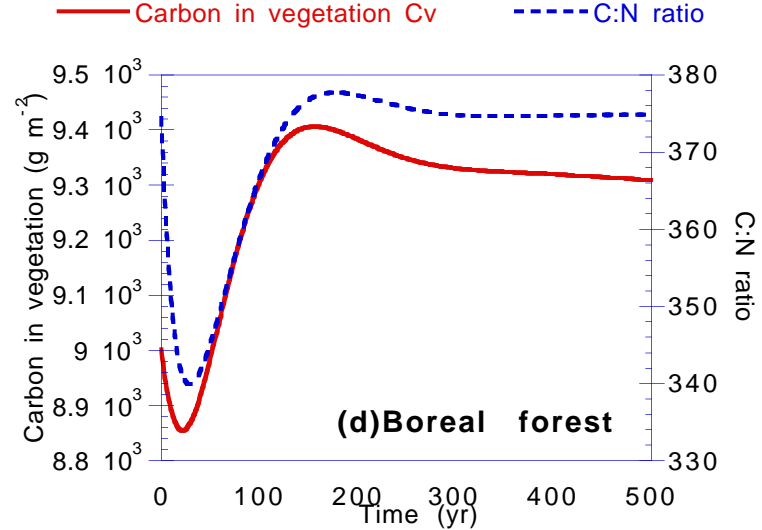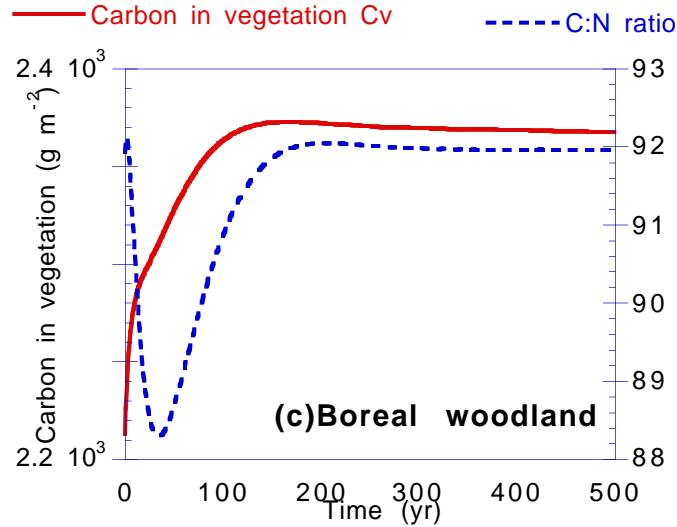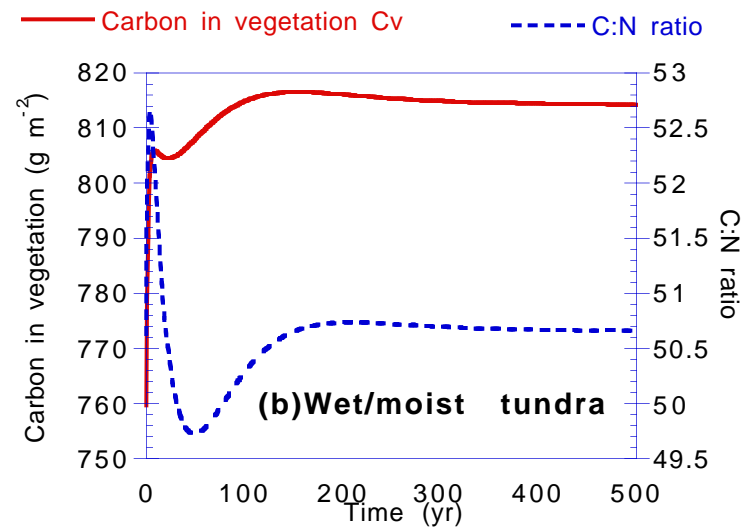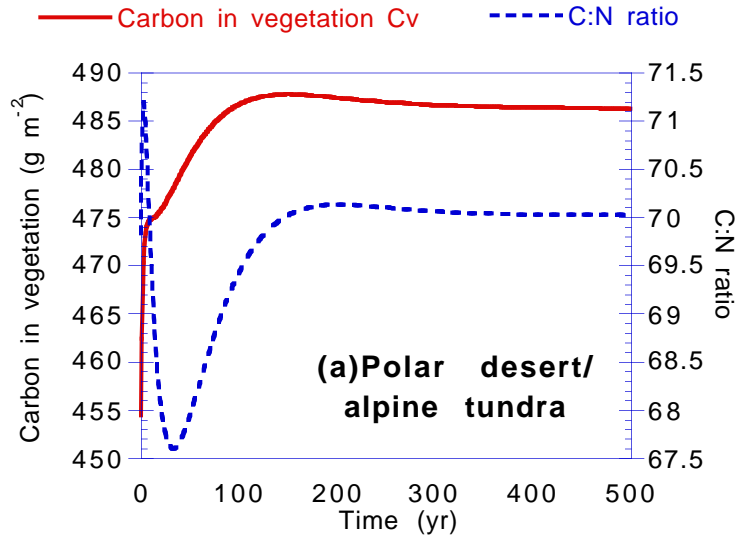
Fig. 13. The transient response of carbon in vegetation and the C:N ratio is shown for a 1˚C temperature rise at time t=0. For previous times the systems were in steady state.
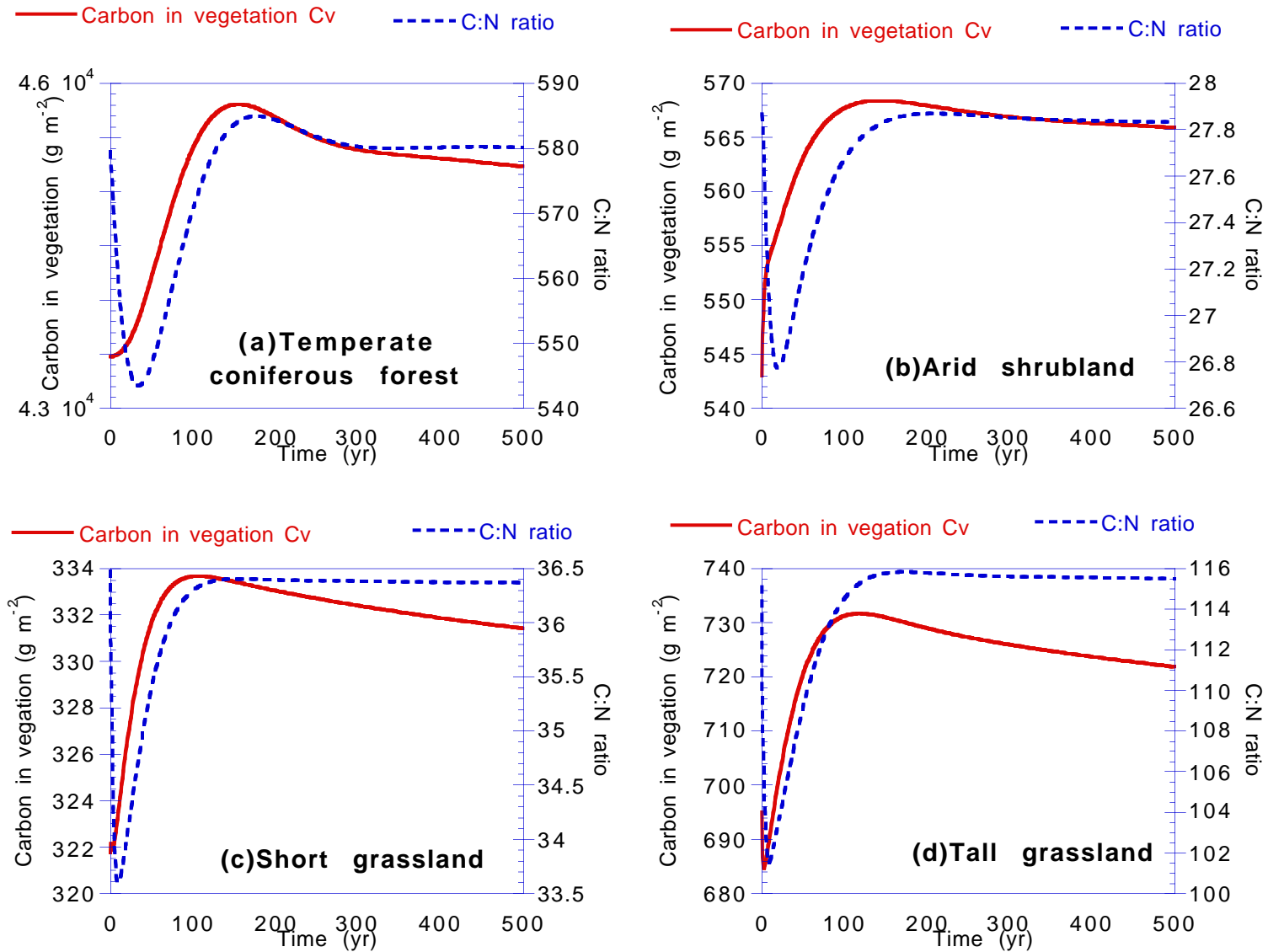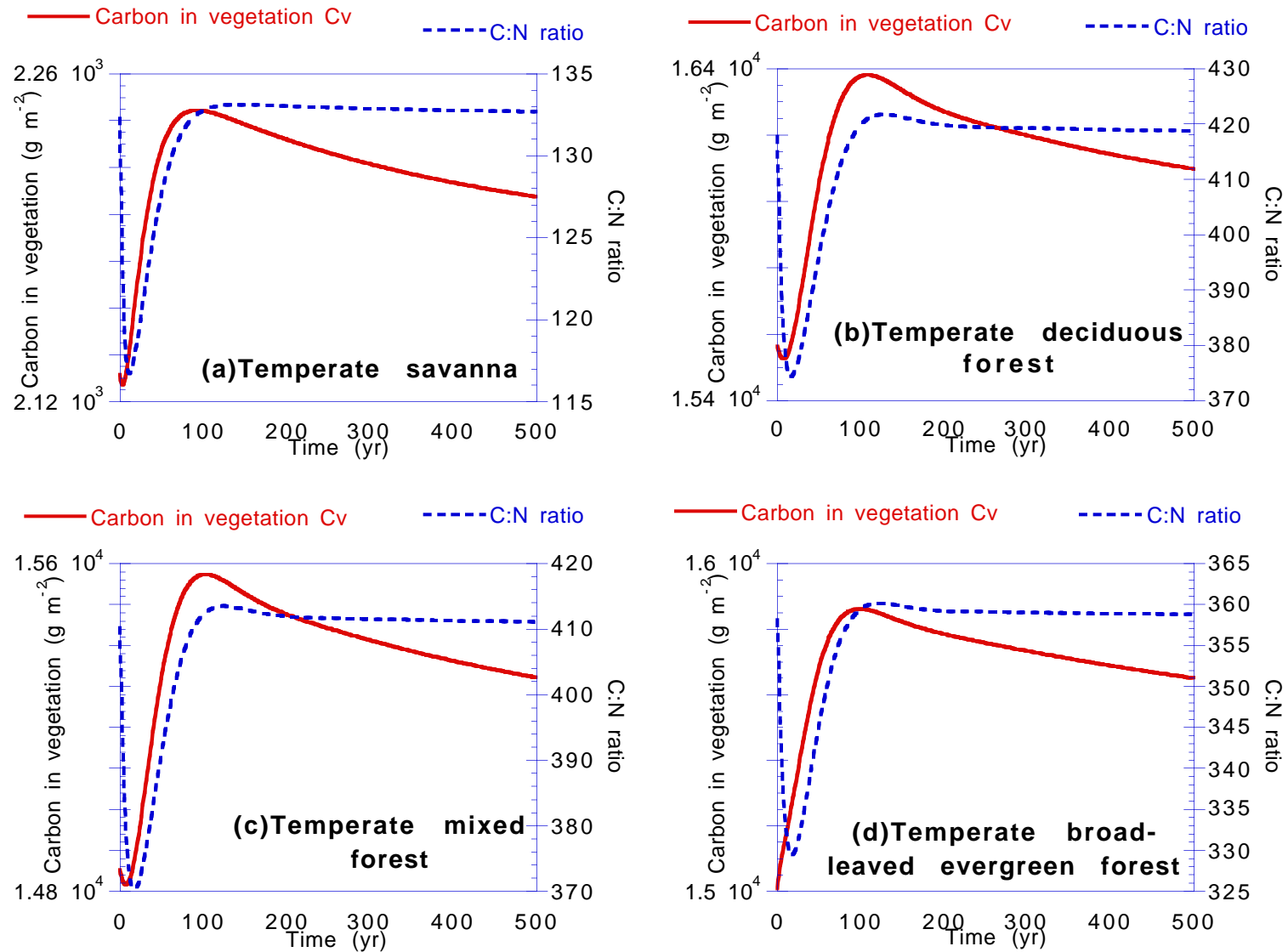
Fig. 14. The transient response of carbon in vegetation and the C:N ratio is shown for a 1˚C temperature rise at time t=0. For previous times the systems were in steady state.
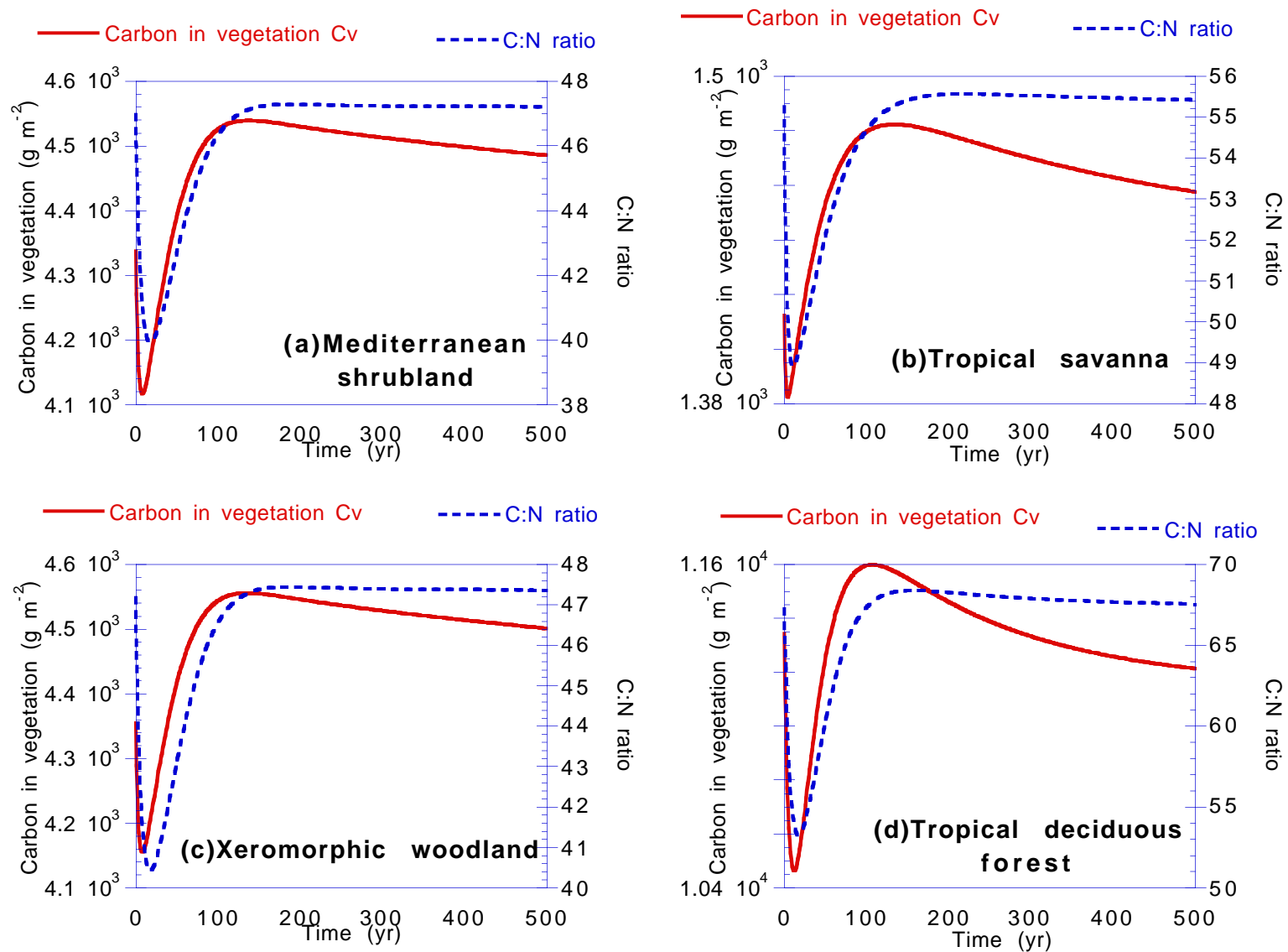
Fig. 15. The transient response of carbon in vegetation and the C:N ratio is shown for a 1˚C temperature rise at time t=0. For previous times the systems were in steady state.

Fig. 16. The transient response of carbon in vegetation and the C:N ratio is shown for a 1°C temperature rise at time t=0. For previous times the systems were in steady state.
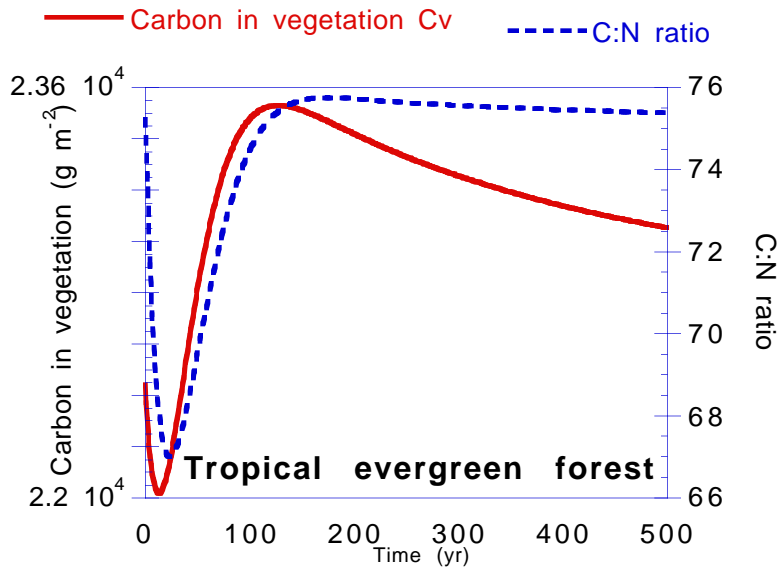
Fig. 17. Transient response of the tropical evergreen forest to a 1˚C increase in temperature at time t=0. The system is initially in steady state and is followed for 500 years subsequent to the perturbation.

increase in respiration dominates and there is a response of *npp* to decrease for increasing temperature even under CO_2 doubling.

    Transient response of the model systems to temperature change.–In Figs. 13 through 17, we show the transient response of carbon in vegetation C_v for each of the 17 systems to a hypothetical instantaneous increase in temperature of 1˚C at t=0. Before t=0, each system is in steady state. For convenience in analyzing these diagrams, we divide the time into three segments: the first year, the next 10 to 150 years until C_v reaches a maximum, and the time following the maximum in C_v to 500 years. The response of C_v to temperature depends on the effect that temperature changes have on gross primary productivity f_T, plant respiration, internal leaf CO_2 C_i, and the ratio of carbon to nitrogen in vegetation which ultimately determines *ac*. The value of nitrogen in vegetation N_v depends on nitrogen dynamics in the soil which, in turn, depends of soil respiration and decomposition. Because of the wide variety of climates and properties of vegetation that occur at the calibration sites, many of possible types of responses of C_v are represented by the 17 sites.

    During the first year, the increase in *gpp* exceeds the increase in plant respiration for the two tundras, boreal woodland, arid shrubland, and temperate broad-leaved evergreen forest leading to an increase in carbon in vegetation C_v. (Of these, the two tundra systems and the boreal woodland are unique because during the first year carbon in vegetation increased so much that the C:N ratio actually increased. Of the 17 sites, this only occurred at the two tundra sites by a significant amount. There was a slight increase in the boreal woodland. In the other 14 sites, the C:N ratio decreased during the first year and for several subsequent years until a minimum C:N ratio was reached between about 10 and 50 years after the temperature change.) During the first year there is only a slight or no excess of gross primary production over plant respiration in short grassland and temperate coniferous forest. Thus the immediate changes in gross primary production and plant respiration due to the direct effect of temperature are more or less in balance for these two systems. For the other 10 systems, the net effect of plant respiration and gross primary productivity produces a decrease in carbon in vegetation C_v. In the temperate mixed forest,

temperate deciduous forest, and temperate savanna, the net decrease in C_v is very modest during the first year. In the boreal forest, the net decrease in C_v in the first year is larger than for the temperate systems. For the other six systems (tall grassland and subtropical and tropical systems), the net decrease of C_v during the first year is sharp and marked.

During the second time period, the C:N ratio in vegetation is falling down to a minimum and the subsequently rises back to the nominal value as gross primary productivity and nitrogen uptake are adjusted by changes in ac to bring the C:N ratio back to the nominal value. As long as the C:N ratio is not at the nominal value, ac changes in the direction designed to bring the C:N ratio back to its nominal value. As this process proceeds, the ac value increases which causes gross primary production to increase and nitrogen uptake to decrease. The basis for the decrease in the C:N ratio independent of changes in gross primary productivity and plant respiration is increased uptake of nitrogen by plants from soil. For example note the two temperate evergreen forests in Figs 14a and 15d. We see that in both these cases the C_v values rise initially but the C:N ratios fall. This is caused by increased nitrogen uptake by plants from soil. This nitrogen is becoming available because of increased soil respiration. While the C:N ratio is below V_{cn}, ac increases by eq. A.99. Because ac is increasing, gpp increases and nitrogen uptake decreases. This continues until the C:N ratio returns to V_{cn}. At this point the carbon and nitrogen are in balance, but the system may still be losing carbon because the increased soil respiration may not have brought the soil compartments to steady state.

During the third time period, from when the C:N ratio returns to V_{cn} until the time reaches 500 years, decomposition continues to relax the system to equilibrium. But now ac has been adjusted so that the nitrogen that comes out of the soil organic nitrogen compartment that is available for uptake is more or less in balance with the gross primary production that is taking up carbon. As soil nitrogen is slowly reduced, carbon in vegetation is slowly decreased also. During this third phase, soil nitrogen is slowly being depleted to steady state because of the increased temperature. The variable ac is also slowly falling during this phase. This process occurs in some degree in all systems. In the two tundras and boreal woodland, this rebalancing of soil nitrogen is only by a slight amount and C_v falls only slightly during this period. In other systems, especially the topics but also in the temperate systems, there is somewhat more rapid decrease in soil nitrogen over this period.

We note that in six systems, boreal forest, temperate mixed forest, temperate broad-leaved evergreen forest, Mediterranean shrubland, xeromorphic woodland, and tropical deciduous forest, the steady state value of C_v shows a net decrease for a 1°C temperature increase. In the other 11 systems, the steady state value of C_v shows a net gain with this temperature rise. For these 11 systems, nitrogen plays a role in this result.

We emphasize that the focus of the analysis of the transient response is to elucidate the processes that drive the response. The time scales associated with the dynamical behavior of this formulation of the carbon-nitrogen coupling cannot be accepted without further study of the acclimation process and an experimental determination of the parameter *adapt*.

DISCUSSION

The TEM and TERRA models are designed under the assumption that it is the parameters for the functional processes that define a local terrestrial ecosystem and that these parameters are more or less constant over a vegetation type. To be sure, the standing crops or elemental pools are important in determining the functional parameters of the model, but it is the parameters not the pools that define the model for a vegetation type. The pools can and do change over a vegetation type but not the parameters. This

assumption is asserted without proof or demonstration and we suggest that it is an area that deserves much more detailed study and experimentation.

These models are also developed under the corollary assumption that the model parameters are constant across a vegetation type no matter where that type is found on the globe. That is, a tropical evergreen forest in South America, Africa, or Borneo all have the same parameters; likewise for Mediterranean shrubland in California, Chile, South Africa, Greece, or Australia. An alternative approach is to "regionalize" the global model in addition to the "biomization" that has already been done in constructing the model around 17 vegetation types. In a "regionalized" approach, one would determine parameters for each vegetation type for a specific region. The same vegetation type in a different region would be calibrated separately. Because such a program would involve more work in constructing a global model, a separate investigation into this approach should be undertaken before it is attempted. Raich et al. (1991) did make a start in this analysis by examining the calibration of tropical evergreen forests from six different sites (one in the Caribbean, two in South America, two in Africa, and one in Malaysia). They found substantial differences in the parameters between the six sites. The parameters C_{max}, K_d, K_{fall}, N_{max}, and N_{up} had coefficients of variation of 0.34, 0.24, 0.28, 0.32, and 0.54, respectively. These preliminary results suggest that more consideration be given to this problem. We believe that the approach used by TEM and TERRA for global biogeochemical cycling has much merit, but one should be mindful of its assumptions and possible limitations.

The calibration scheme is producing internally consistent results. The good correlation (correlation coefficient of 0.83) between C_{max} and lai_{max} is one example of this consistency. This particular consistency is achieved because we have introduced a process-based water budget model and have modified the connection between the water model and the gpp calculation. The effect of the water balance model on gross primary productivity is communicated by the stomatal conductance variable cd (approximated by the ratio of actual to potential transpiration to preserve the flavor of TEM). Using this realistic method of expressing the effect of water stress on gross primary productivity means that C_{max} does not have to compensate for the error in using a less accurate method. Hence, C_{max} remains well-correlated with lai_{max}.

Even though TERRA is a relatively simple model with few state variables, it includes enough responsiveness to variation in forcing variables such as temperature, precipitation, and light that the seasonal dynamics of carbon in vegetation clearly shows differences from site to site. The annual average values of C_v in Fig. 5 shows site differences that derive from the vegetation-type specific parameters and intersite variation in climate and soils. In Fig. 5, we recover the obvious differences in average C_v between forests, woodlands, savannas, grasslands, shrublands, and tundra that were used to develop the model initially. The timing of the phases of the annual variation is driven by temperature and light in the high latitude and moist temperate zones. The dry temperate zones are driven by temperature, precipitation, and light. In the tropics, precipitation is the key variable in annual variation. The seasonal responses are even more clearly demonstrated in the results for net primary production. In the high latitude systems, the timing (or phase) and amplitude of net primary production is driven by temperature and light. In the temperate systems, temperature is a dominant factor, but in water-limited temperate systems the timing of precipitation begins to play a co-dominant role with temperature in determining net primary production. In the tropic sites, precipitation is an overwhelming factor in net primary production amplitude and timing. Similar conclusions can be drawn from Fig. 7 of cumulative net ecosystem production. Recall that net ecosystem production is net primary production minus soil respiration. In the high latitude and temperate systems, we see the dominant effect of temperature on soil respiration. In the tropics, often soil moisture rather than temperature drives the variation in soil respiration over the year; just as precipitation drives the timing of net primary production in

these systems. (In the particular case of the tropical deciduous forest in India, the site was at about 25°N and there is significant temperature variation over the course of the year as well as extreme precipitation variation over the year.). The variation in soil moisture and the ratio of actual to potential transpiration shown in Figs. 8 through 12 when compared to Fig. 7 supports these conclusions. In general we find good qualitative agreement between the model results of soil moisture and field observation for these systems. The strong variation in soil moisture and the ratio of actual to potential transpiration during dry seasons for these systems emphasizes the importance of including realistic water balance calculations when projecting production.

From the sensitivity of the steady state response of the model to changes in model parameters, we conclude that Q_{10} (except in the high latitudes) and the parameters that determine the effect of soil moisture on soil respiration are key parameters in predicting future levels of CO_2. Furthermore, as a rule the calibration parameters (overall coefficients for each flux of carbon and nitrogen) are also key parameters in model performance. This suggests that future research resources be used to accurately quantify these fluxes. This effort should be made at calibration sites or at any sites used to test or extend the applicability of the model. The other parameters of substantial importance are the parameters for the Michaelis-Menten response for nitrogen uptake k_{n1} and CO_2 uptake k_{CO2}. These two parameters are of ubiquitous importance and should be measured for each system.

Response of the model to environmental changes

The TERRA model exhibited a fertilization response to increases in nitrogen inputs. A 10% increase in nitrogen deposition produced about a 2.3±0.9% increase in carbon sequestration averaged over the 17 systems. More importantly it was found that on the basis of a fixed amount applied, there was substantial difference across the systems with the tundra, boreal, and temperate evergreen forests sequestering over 10^4 gC at steady state for every gram of nitrogen added per year. These results suggest that increased nitrogen inputs to the terrestrial biosphere might be an important factor in increased carbon sequestration and may be part of the explanation for the "missing sink" problem. This is in agreement with the conclusions of Hudson et al. (1994) that suggest that nitrogen deposition may constitute an important source of fertilization for the terrestrial biosphere. Furthermore increasing CO_2 by 10% also produced an increase in carbon sequestration of 1.9±0.4% averaged across the 17 systems. These results also suggest that the fertilization effect of increasing CO_2 must be included in a calculation of the "missing sink" problem. We believe that TERRA could be used to explore the effects of global changes in nitrogen deposition and CO_2 levels on global patterns of seasonal variation in CO_2 levels and on global patterns of sources and sinks of carbon.

The model results suggest that any future increases in precipitation will have the net effect of increasing carbon storage in most systems. Already wet systems experience little or no increase in production and can experience a decrease in total carbon storage due to increased moisture. In some dry systems, e.g., arid shrubland, paradoxically the increase in carbon storage in vegetation with higher rainfall is more than offset by a decrease in soil carbon under wetter conditions. In future work, TERRA could be used to explore the effect of precipitation changes in the global carbon budget using the full global model. This current sensitivity exercise suggests, on balance, a net sequestration of carbon would occur for the global system for increased precipitation.

Doubling CO_2 by itself produces a 12±2% increase in both carbon storage and in net primary production averaged across all 17 systems. Note that this increase is actually greater for some systems (systems 2 through 7 except for the boreal forest system 4) under a concomitant temperature rise. All other systems, especially in the tropics show a marked decrease with temperature in the amount of carbon storage that is enhanced under a CO_2

75

doubling. The systems that experience a sequestration effect for increases in both temperature and CO_2 are cold systems with nutrient limitations. These systems experienced an increase in productivity (at least in part) due to a speed up of the release of nitrogen by soil decomposition.

The 12±2% increase in net primary production for the 17 systems is substantially less than the 23% increase in *npp* which would nominally occur for the value of k_{CO2} used here. This difference between the nominal 23% and the realized 12% is due to other limiting factors in the various systems.

Change in temperature can produce a direct, immediate effect on gross primary production (typically an increase in *gpp* occurs for an increase in temperature, but a decrease in *gpp* is possible in principle) and a direct, immediate effect in plant respiration. Changing the temperature affects the vapor pressure deficit which directly changes transpiration and changes the stomatal conductivity, because of the change in vapor pressure deficit, which also changes transpiration. These changes affect the uptake of CO_2 by the plant and gross primary productivity. Finally, changing the temperature can affect the decomposition rate in the soil and the release (mineralization) of nitrogen by decomposition and also the immobilization rate. These changes alter the availability of nitrogen to the plant and can result in a fertilization effect for increasing temperature. These processes combine to produce the variation between figures in Figs 13 through 17 and the variation over systems in the results in Tables 20 and 21. We emphasize that the relative importance of the effect on net primary productivity of increased mineralization due to increased temperature shows a strong interaction with other properties of the calibration sites or vegetation types. Even though increased mineralization rates resulting from increased temperature occur for all systems, other processes affected by temperature (e.g., plant respiration) can dominate the effect of temperature on net primary production depending on the system or site. The degree to which nitrogen is limiting in a particular system may be a factor determining the relative importance of increasing the mineralization rate. The complex interactions between processes affecting production that are dependent on temperature require further study. The results on the effects of increased temperature in nitrogen-limited systems have important consequences for future projections of atmospheric CO_2 levels.

ACKNOWLEDGMENTS

REFERENCES

Aber, J.D. and J.M. Melillo. 1980. Litter decomposition: measuring relative contributions of organic matter and nitrogen to forest soils. Canadian Journal of Botany 58:416-421.

Aber, J.D. and J.M. Melillo. 1982. Nitrogen immobilization in decaying hardwood leaf litter as a function of initial nitrogen and lignin content. Canadian Journal of Botany 60:2263-2269.

Aber, J.D., J.M. Melillo, C.A. McClaugherty, and K.N. Eshleman. 1983. Potential sinks for mineralized nitrogen following disturbance in forest ecosystems. Ecological Bulletin (Stockholm) 35:179-192.

Agren, G.I., R.E. McMurtrie, W.J. Parton, J. Pastor, and H.H. Shugart. 1991. State-of-the-art of models of production-decomposition linkages in conifer and grassland ecosystems. Ecological Applications 1:118-138.

Allen, L.H.,Jr., and E.R. Lemon. 1976. Carbon dioxide exchange and turbulence in a Costa Rican tropical rain forest. p. 265-308. *In* Vegetation and the Atmosphere. Volume 2. Case Studies. (J.L. Monteith, ed.) Academic Press, New York.

Auclair, A.N.D. and A.N. Rencz. 1982. Concentration, mass, and distribution of nutrients in a subarctic *Picea mariana-Cladonia alpestris* ecosystem. Canadian Journal of Forest Research 12:947-968.

Aylett, G.P. 1985. Irradiance, interception, leaf conductance and photosynthesis in Jamaican upper montane rain forest trees. Photosynthetica 19:323-337.

Bacastow, R., and C.D. Keeling. 1973. Atmospheric carbon dioxide and radiocarbon in the natural carbon cycle. Changes from A.D. 1700 to 2070. p. 86-135. *In* Carbon and the Biosphere (G.M. Woodwell and E.V. Pecan, eds.) CONF-720510, Atomic Energy Commission, Washington, D.C.

Bandhu, D. 1970. A study of the productive structure of northern tropical dry deciduous forests near Varanasi. I. Stand structure and non-photosynthetic biomass. Tropical Ecology 11:90-104.

Barnes, P.W. 1985. Adaptation to water stress in the big bluestem-sand bluestem complex. Ecology 66:1908-1920.

Bierlmaier, F.A. and A. McKee. 1989. Climatic summaries and documentation for the primary meteorological station, H.J. Andrews Experimental Forest, 1972 to 1984. USDA Forest Service, Pacific Northwest Research Station, General Technical Report PNW-GTR-242.

Bjerregaard, R.S. 1971. The nitrogen budget of two salt desert shrub plant communities of western Utah. Ph.D. dissertation, Utah State University. University Microfilms, Ann Arbor, MI. 100 p.

Blake-Jacobson, M.E. 1987. Stomatal conductance and water relations of shrubs growing at the chaparral-desert ecotone in California and Arizona. p. 223-246. *In* Plant Responses to Stress: Functional Analysis in Mediterranean Ecosystems. NATO ASI Series G: Ecological SciencesVol. 15. (J.D. Tenhunen, F.M. Catarino, O.L. Lange, and W.C. Oechel, eds.) Springer-Verlag, New York.

Bokhari, U.G. and J.S. Singh. 1975. Standing state and cycling of nitrogen in soil-vegetation components of prairie ecosystems. Annals of Botany 39:273-285.

Bonan, G.B., H.H. Shugart, and D.L. Urban. 1990. The sensitivity of some high-latitude boreal forests to climatic parameters. Climatic Change 16:9-29.

Bowden, R.D., J.M. Melillo, P.A. Steudler, and J.D. Aber. 1991. Effects of nitrogen additions on annual nitrous oxide fluxes from temperate forest soils in the northeastern United States. Journal of Geophysical Research 96D:9321-9328.

Brown, J, K.R. Everett, P.J. Webber, S.F. MacLean, Jr., and D.E. Murray. 1980. The coastal tundra at Barrow. p. 1-29. *In* An Arctic Ecosystem. The Coastal Tundra at

Barrow, Alaska. US/IBP Synthesis Series 12. (J. Brown, P.C. Miller, L.L. Tieszen, and F.L. Bunnell, eds.) Dowden, Hutchinson, & Ross, Stroudsberg, Pennsylvania.

Burk, J.H. 1988. Sonoran desert vegetation. p. 869-892. *In* Terrestrial Vegetation of California (M.G. Barbour and J. Major, eds.) California Native Plant Society, Sacramento, California.

Burton, A.J., K.S. Pregitzer, and D.D. Reed. 1991. Leaf area and foliar biomass relationships in northern hardwood forests located along an 800 km acid deposition gradient. Forest Science 37:1041-1059.

Caldwell, M.M., R.S. White, R.T. Moore, and L.B. Camp. 1977. Carbon balance, productivity, and water use of cold-winter desert shrub communities dominated by C_3 and C_4 species. Oecologia (Berl.) 29:275-300.

Carter, G.A., W.K. Smith, and J.L. Hadley. 1988. Stomatal conductance in three conifer species at different elevations during summer in Wyoming. Canadian Journal of Forest Research 18:242-246.

Chapin, F.S., III. and G.R. Shaver. 1985. Individualistic growth response of tundra plant species to environmental manipulations in the field. Ecology 66:564-576.

Chiariello, N. 1984. Leaf energy balance in the wet lowland tropics. p. 85-98. *In* Physiological Ecology of Plants in the Wet Tropics. Tasks for Vegetation Science 12. (E. Medina, H.A. Mooney, and C. Vazquez-Yanes, eds.) Dr. W. Junk Publishers, Boston.

Ciais, P., P.P. Tans, J.W.C. White, M. Trolier, R.J. Francey, J.A. Berry, D.R. Randall, P.J. Sellers, J.G. Collatz, and D.S. Schimel. 1995. Partitioning of ocean and land uptake of CO_2 as inferred by $\delta^{13}C$ measurements from the NOAA Climate Monitoring and Diagnostics Laboratory Global Air Sampling Network. Journal of Geophysical Research 100D:5051-5070.

Clark, F.E. 1977. Internal cycling of ^{15}Nitrogen in shortgrass prairie. Ecology 58:1322-1333.

Conant, S. and P.G. Risser. 1974. Canopy structure of a tall-grass prairie. Journal of Range Management 27:313-318.

Correia, O., F. Catarino, J.D. Tenhunen, and O.L. Lange. 1987. Regulation of water use by four species of *Cistus* in the scrub vegetation of the Serra da Arrabida, Portugal. p. 247-258. *In* Plant Responses to Stress: Functional Analysis in Mediterranean Ecosystems. NATO ASI Series G: Ecological SciencesVol. 15. (J.D. Tenhunen, F.M. Catarino, O.L. Lange, and W.C. Oechel, eds.) Springer-Verlag, New York.

Dannevik, W.P., W. Emanuel, J. Ambrosiano, J.R. Kercher, J.E. Penner. 1994. CERES Progress Report: Phases I and II. UCRL-ID-116573. Lawrence Livermore National Laboratory, Livermore, CA.

Davis, S.D. and H.A. Mooney. 1985. Comparative water relations of adjacent California shrub and grassland communities. Oecologia (Berlin) 66:522-529.

Day, T.A., E.H. DeLucia, and W.K. Smith. 1989. Influence of cold soil and snowcover on photsynthesis and leaf conductance in two Rocky Mountain conifers. Oecologia (Berlin) 80:546-552.

DeAngelis, D.L., R. H. Gardner, and H.H. Shugart, Jr. 1981. Productivity of forest ecosystems studied during IBP: the woodlands data set. p. 567-672. *In* Dynamic Properties of Forest Ecosystems. International Biological Programme 23. (D.E. Reichle, ed.) Cambridge University Press, New York.

DeLucia, E.H. and W. H. Schlesinger. 1990. Ecophysiology of Great Basin and Sierra Nevada vegetation on contrasting soils. p. 143-178. *In* Plant Biology of the Basin and Range. Ecological Studies 80 (C.B.Osmond, L.F. Pitelks, G.M.Hidy, eds.) Springer-Verlag, New York.

Dennis, J.G., L.L. Tieszen, and M.A. Vetter. 1978. Seasonal dynamics of above- and belowground production of vascular plants at Barrow, Alaska. p. 113-140. *In*

Vegetation and Production Ecology of an Alaskan Arctic Tundra (L.L. Tieszen, ed.) Springer-Verlag, New York.

De Lillis, M. and G.C. Sun. 1990. Stomatal response patterns and photosynthesis of dominant trees in a tropical monsoon forest. Acta Oecologica 11:545-555.

Dickinson, R.E., A. Henderson-Sellers, P.J. Kennedy, and M.F. Wilson. 1986. Biosphere-atmosphere transfer scheme (BATS) for the NCAR community climate model. NCAR Technical Note NCAR/TN-275+STR, Atmosph. Analysis and Prediction Div., National Center for Atmospheric Research, Boulder, Colorado. 69 p.

Dignon, J., J.R. Kercher, J.E. Penner, and J.J. Walton. 1995. The carbon cycle: results of a coupled atmospheric chemical tracer transport model and an ecosystem model. 8th CACGP Symposium and 2nd IGAC Scientific Conference Fuji-Yoshida, Japan Sept 5-9, 1994.

Dolman, A.J., J.H.C. Gash, J.R. Shuttleworth, and W.J. Shuttleworth. 1991. Stomatal and surface conductance of tropical rainforest. Agricultural and Forest Meteorology 54:303-318.

Doorenbos, J. and W.O. Pruitt. 1977. Guidelines for prediction of crop water requirements. FAO Irrig. and Drain. Paper No. 24, 2nd ed., Food and Agriculture Organization, Rome, Italy. 156 p.

Dunin, F.X., A.R. Aston, and W. Reyenga. 1978. Evaporation from a *Themeda* grassland. II. Resistance model for plant evaporation. Journal of Applied Ecology 15:847-858.

Dutch, M.E., and J.D. Stout. 1968. The carbon cycle in a beech forest ecosystem in relation to microbial and animal populations. p. 37-48. In 9th International Congress of Soil Science Transactions (Adelaide, Australia 1968) Vol II. Int'l. Soc. of Soil Science and Angus and Robertson, Sydney, Australia.

Earth System Sciences Committee. 1988. Earth System Science. A Program for Global Change. NASA Advisory Council, National Aeronautics and Space Administration, Washington, D.C.

Edwards, P.J. and P.J. Grubb. 1977. Studies of mineral cycling in a Montane Rain forest in New Guinea. I. The distribution of organic matter in the vegetation and soil. Journal of Ecology 65:943-970.

Ehleringer, J. and H.A. Mooney. 1983. Productivity of desert and Mediterranean-climate plants. p. 233-280. *In* Physiological Plant Ecology IV. Ecosystem Processes: Mineral Cycling, Productivity and Man's Influence. Encyclopedia of Plant Physiology New Series Volume 12D. (O.L. Lange, P.S. Nobel, C.B. Osmond, and H. Ziegler, eds.) Springer-Verlag, New York.

Esser. G. 1987. Sensitivity of global carbon pools and fluxes to human and potential climatic impacts. *Tellus* 39B:245-260.

Esser, G. 1991. Osnabruck Biosphere Model: structure, construction, results. p. 679-710. *In* Modern Ecology (G.Esser and D. Overdieck. eds.) Elsevier, New York.

Federer, C.A., and G.W. Gee. 1976. Diffusion resistance and xylem potential in stressed and unstressed northern hardwood trees. Ecology 57:975-984.

Fetcher, N. 1979. Water relations of five tropical tree species on Barro Colorado Island, Panama. Oecologica (Berl.) 40:229-233.

Foley, J.A. 1994. Net primary productivity in the terrestrial biosphere: the application of a global model. Journal of Geophysical Research 99D:20773-20783.

Forseth, I.N., J.R. Ehleringer, K.S. Werk, and C.S. Cook. 1984. Field water relations of Sonoran Desert annuals. Ecology 65:1436-1444.

Francey, R.J., P.P. Tans, C.E. Allison, I.G. Enting, J.W.C. White, and M. Trolier. 1995. Changes in oceanic and terrestrial carbon uptake since 1982. Nature 373:326-330.

Frost, P.G.H. 1985. Organic matter and nutrient dynamics in a broadleaved African savanna. p. 200-206. *In* Ecology and Management of the World's Savannas (J.C. Tothill and J.J. Mott, eds.) Australian Academy of Science, Canberra, Australia.

Gates, D.M. 1980. Biophysical Ecology. Springer-Verlag, New York. 611 p.

Gates, D.M. 1985. Global biospheric response to increasing atmospheric carbon dioxide concentration. p. 171-184. *In* Direct Effects of Increasing Carbon Dioxide on Vegetation (B.R. Strain and J.D. Cure, eds.) DOE/ER-0238. U.S. Department of Energy, Washington, D.C.

Geiger, R. 1965. World Atmosphere Series of Maps, Map No. WA6: Annual Effective Evapotranspiration. Darmstadt: Justus Perthes.

Gentry, A.H. 1993. A Field Guide to the Families and Genera of Woody Plants of Northwest South America. Conservation International, Washington, D.C. 895 p.

Gibbs-Russell, G.E., L. Watson, M. Koekemoer, L. Smook, N.P. Barker, H.M. Anderson, and M.J. Dallwitz. 1990. Grasses of Southern Africa. Memoirs of the Botanical Survey of South Africa No. 58. National Botanic Gardens, South Africa. 437 p.

Giblin, A.E., K.J. Nadelhopper, G.R. Shaver, J.A. Laundre, and A.J. McKerrow. 1991. Biogeochemical diversity along a riverside toposequence in Arctic Alaska. Ecological Monographs 61:415-435.

Goldstein, G.H., L.B. Brubaker, and T.M. Hinckley. 1985. Water relations of white spruce (*Picea glauca* (Moench) Voss) at tree line in north central Alaska. Canadian Journal of Forest Research 15:1080-1087.

Gollan, T., N.C. Turner, and E.-D. Schulze. 1985. The responses of stomata and leaf gas exchange to vapor pressure deficits and soil water content. III. In the sclerophyllous woody species *Nerium oleander*. Oecologia (Berlin) 65:356-362.

Graham, J.S. and S.W. Running. 1984. Relative control of air temperature and water stress on seasonal transpiration of Pinus contorta. Canadian Journal of Forest Research 14:833-838.

Grier, C.C. and R.S. Logan. 1977. Old-growth *Pseudotsuga menziesii* communities of a western Oregon watershed: biomass distribution and production budgets. Ecological Monographs 47:373-400.

Grigal, D.F., L.M. Chamberlain, H.R. Finney, D.V. Wroblewski, and E.R. Gross. 1974. Soils of the Cedar Creek Natural History Area. Miscellaneous Report 123, Agricultural Experiment Station, University of Minnesota, St. Paul, MN.

Hanes, T.L. 1988. Chaparral. p. 417-470. *In* Terrestrial Vegetation of California (M.G. Barbour and J. Major, eds.) California Native Plant Society, Sacramento, California.

Harlow, W.M. and W.S. Harrar. 1969. Textbook of Dendrology. McGraw-Hill, New York. 512 p.

Haugen, R. K. 1982. Climate of Remote Areas of North-central Alaska: 1975-1979 Summary. CRREL Report 82-35. U.S. Army Cold Regions Research and Engineering Laboratory, Hanover, New Hampshire. 114 p.

Hooker, J.D. 1875. The Flora of British India. Vols I-VII. Reprinted 1973. Periodical Experts, Delhi, India. 5568 p.

Houghton, R.A. 1989. The long-term flux of carbon to the atmosphere from changes in land use. Environmental Pollution Monitoring and Research Program Publication No. 59, World Meteorlgical Organiztion, Geneva.

Hudson, R.J.M., S.A. Gherini, and R.A. Goldstein. 1994. Modeling the global carbon cycle: Nitrogen fertilization of the terrestrial biosphere and the "missing" CO_2 sink. Global Biogeochemical Cycles 8:307-333.

Huntley, B.J. and J.W. Morris. 1982. Structure of the Nylsvley Savanna. p. 433-455. *In* Ecology of Tropical Savannas. Ecological Studies 42. (B.J. Huntley and B.H. Walker, eds.) Springer-Verlag, New York.

Jarvis, P.G., G.B. James, and J.J. Landsberg. 1976. Coniferous forest. p. 171-240. *In* Vegetation and the Atmosphere. Volume 2. Case Studies. (J.L. Monteith, ed.) Academic Press, New York.

Jarvis, P.G., H.S. Miranda, and R.I. Muetzelfeldt. 1985. Modelling canopy exchanges of water vapor and carbon dioxide in coniferous forest plantations. p. 521-542. *In* The Forest-Atmosphere Interaction (B.A. Hutchison and B.B. Hicks, eds.) D. Reidel Publishing Co., Boston.

Jarvis, P.G. and J.W. Leverenz. 1983. Producitivity of temperate, deciduous and evergreen forests. p. 233-280. *In* Physiological Plant Ecology IV. Ecosystem Processes: Mineral Cycling, Productivity and Man's Influence. Encyclopedia of Plant Physiology New Series Volume 12D. (O.L. Lange, P.S. Nobel, C.B. Osmond, and H. Ziegler, eds.) Springer-Verlag, New York.

Jensen, M.E., R.D. Burman, and R.G. Allen. 1990. Evapotranspiration and Irrigation Water Requirements. ASCE Manuals and Reports on Engineering Practice No. 70. American Soc. of Civil Eng., New York. 332 p.

Johnson, D.A. and M.M. Caldwell. 1976. Water potential components, stomatal function, and liquid phase water transport resistances of four arctic and alpine species in relation to moisture stress. Physiologia Plantarum 36:271-278.

Jurik, T.W. 1986. Seasonal patterns of leaf photosynthetic capacity in successional northern hardwood tree species. American Journal of Botany 73:131-138.

Kansa, E.J., M. C. Axelrod, and J.R. Kercher. 1994. Interpolation of scattered temperature data measurements onto a worldwide regular grid using radial basis functions with applications to global warming. p. 254-256. In 14th IMACS World Congress on Computational and Applied Mathematics: Vol. 1. (W.F. Ames, ed.) International Association for Mathematics and Computers in Simulation.

Kapos, V. and E.V.J. Tanner. 1985. Water relations of Jamaican upper montane rain forest trees. Ecology 66:241-250.

Kauppi, P. and M. Posch. 1985. Sensitivity of boreal forests to possible climatic warming. Climatic Change 7:45-54.

Keay, R.W. 1989. Trees of Nigeria. Clarendon Press, Oxford. 476 p.

Keeling, C.D. 1973. The carbon dixoide cycle: reservoir models to depict the exchange of atmospheric carbon dioxide with the oceans and land plants. p. 251-329. *In* Chemistry of the Lower Atmosphere (S.I. Rasool, ed.) Plenum Press, New York.

Keeling, C.D., R.B. Bacastow, A.F. Carter, S.C. Piper, T.P. Whorf, M. Heimann, W.G. Mook, and H.A. Roeloffzen. 1989. A three dimensional model of atmospheric CO_2 transport based on observed winds. 1. Analysis of observational data. p. 165-236. *In* Aspects of Climate Variability in the Pacific and Western Americas (D.H. Peterson, ed.) Geophysical Monograph Series 55, American Geophysical Union, Washington, D.C.

Kelliher, F.M., R. Leuning, and E.-D. Schulze. 1993. Evaporation and canopy characteristics of coniferous forests and grasslands. Oecologia 95:153-163.

King, A.W. and D.L. DeAngelis. 1985. Information for seasonal models of carbon fluxes in terrestrial biomes. ORNL/TM-9404. Oak Ridge National Laboratory, Oak Ridge, TN.

King, A.W. and D.L. DeAngelis. 1986. Site-specific seasonal models of carbon fluxes in terrestrial biomes. ORNL/TM-9749. Oak Ridge National Laboratory, Oak Ridge, TN.

King, A.W. and D.L. DeAngelis. 1987. Information for seasonal models of carbon fluxes in agroecosystems. ORNL/TM-9935. Oak Ridge National Laboratory, Oak Ridge, TN.

Kinyamario, J.I. and S.K. Imbamba. 1992. Savanna at Nairobi National Park, Nairobi. p. 25-69. *In* Primary Productivity of Grass Ecosystems of the Tropics and Sub-tropics. (S.P. Long, M.B. Jones, and M.J. Roberts, eds.) Chapman and Hall, New York.

Klinge, H. 1976, Bilanzierung von hauptnahrstoffen im okosystem tropischer regenwald (Manaus) vorlaufige daten. Biogeographica 7:59-77.

Knapp, A.K. 1985. Effect of fire and drought on the ecophysiology of *Andropogon gerardii* and *Panicum virgatum* in a tallgrass prairie. Ecology 66:1309-1320.

Knapp, A.K. and W.K. Smith. 1987. Stomatal and photosynthetic responses during sun/shade transitions in subalpine plants: influence on water use efficiency. Oecologia (Berlin) 74:62-67.

Kohlmaier, G.H., E.-O. Sire, A. Janecek, C.D. Keeling, S.C. Piper, and R. Revelle. 1989. Modelling the seasonal contribution of a CO_2 fertilization effect of the terrestrial vegetation to the amplitude increase in atmospheric CO_2 at Mauna Loa Observatory. Tellus 41B:487-510.

Korner, Ch. 1994. Leaf diffusive conductances in the major vegetation types of the globe. p. 463-490. *In* Ecophysiology of Photosynthesis. Ecological Studies 100. (E.-D. Schulze and M.M. Caldwell, eds.) Springer-Verlag, New York.

Korner, Ch. and P.M. Cochrane. 1985. Stomatal responses and water relations of Eucalyptus pauciflora in summer along an elevational gradient. Oecologia (Berlin) 66:443-455.

Korner, Ch., A. Allison, and H. Hilscher. 1983. Altitudinal variation of leaf diffusive conductance and leaf anatomy in heliophytes on montane New Guinea and their interrelation with microclimate. Flora 174:91-135.

Kozlowski, T.T., P.J. Kramer, and S.G. Pallardy. 1991. The Physiological Ecology of Woody Plants. Academic Press, New York. 657 p.

Kummerow, J., G. Montenegro, and D. Krause. 1981. Biomass, phenology, and growth. p. 69-96. *In* Resource Use by Chaparral and Matorral: A Comparison of Vegetation Function in Two Mediterranean Type Ecosystems.Ecological Studies 39. (P.C. Miller, ed.) Springer-Verlag, New York.

Larcher, W., 1991. Physiological Plant Ecology. 2nd Edition. Springer-Verlag, New York.

Laumonier, Y, V. Trichon, J.-P. Gastellu-Etchegorry, and P. Birnbaum. 1991. Heterogeneite geometrique et radiometrique de la canopee: essai de cartographie. p.271-287. *In* Biologie D'une Canopee de Foret Equatoriale-II (F. Halle et O. Pascal, eds.) Ministere de la Recherche de la Technologie, Reserve de Campo, Cameroun.

Leemans, R. and W.P. Cramer. 1992. IIASA mean monthly temperature, precipitation, and cloudiness.p. A03-1 to A03-9. In Documentation Manual Disc-A. Global Ecosystem Database. Report no. EPA/600/R-92/194b (J.J. Kineman and M.A. Ohrenschall, eds.) NOAA, National Geophysical Data Center, Boulder, CO.

Leverenz, J., J.D. Deans, E.D. Ford, P.G. Jarvis, R. Milne, and D. Whitehead. 1982. Sytematic spatial variation of stomatal conductance in a Sitka spruce plantation. Journal of Applied Ecology. 19:835-851.

Lewis, M.C. and T.V. Callaghan. 1976. Tundra. p. 399-433. *In* Vegetation and the Atmosphere. Volume 2. Case Studies. (J.L. Monteith, ed.) Academic Press, New York.

Lieth, H. 1973. Primary production: terrestrial ecosystems. *Human Ecology* 1:303-332

Lieth, H. 1975. Modeling the primary productivity of the world. p. 237-263. *In* Primary Productivity of the Biosphere (H. Leith and R. H. Whittaker, eds.) Springer-Verlag, New York.

Lieth,H. and E. Box. 1972. Evapotranspiration and primary productivity; C.W. Thornthwaite Memorial Model. *Publications in Cllimatology* 25(2):37-46. C.W. Thornthwaite Assoc., Centerton-Elmer, New Jersey.

Long, R.W. and O. Lakela. 1971. A Flora of Tropical Florida. University of Miami Press, Coral Gables, FL. 962 p.

LTERnet. U.S. Long-Term Ecological Research Network. 1995. Harvard Forest Climate Data Set. (Harvard Forest LTER Site. P.O. Box 68, Petersham, MA; http://lternet.edu/~rlent/climate.txt). LTER Network Office, University of Washington, Seattle.

Lugo, A.E. and P.G. Murphy. 1986. Nutrient dynamics of a Puerto Rican subtropical dry forest. Journal of Tropical Ecology 2:55-72.

Lugo, A.E., J.A. Gonzalez-Liboy, B. Cintron, and K. Dugger. 1978. Structure, productivity, and transpiration of a subtropical dry forest in Puerto Rico. Biotropica 10:278-291.

Mass, P.J.M. and L.Y.Th. Westra. 1993. Neotropical Plant Families. Koeltz Scientific Books, Champaign, IL. 289 p.

Marland, G.T., A. Boden, R.C. Griffin, S.F. Huang, P. Kanciruk, and T.R. Nelson. 1989. Estimates of CO_2 emissions fro fossil fuel burning and cement manufacturing, based on United States energy statistics and the US Bureau of Mines cement manufacturing data. ORNL/CDIAC-25, Oak Ridge National Laboratory, Oak Ridge, TN. 60 p.

Matthews, E. 1983. Global vegetation and land use: new high-resolution data bases for climate studies. Journal of Climate and Applied Meteorology 22:474-487.

Matthews, E. 1984. Vegetation, land-use, and seasonal albedo data sets: documentation of archived data tape. NASA Technical Memorandum 86107, National Aeronautics and Space Administration, Goddard Space Flight Center, Institute for Space Studies, New York, NY.12 p.

McGregor, R.L., T.M. Barkley, R.E. Brooks, and E.K. Schofield. 1986. Flora of the Great Plains. University Press of Kansas, Lawrence Kansas. 1392. p.

McGuire, A.D., J.M. Melillo, L.A. Joyce, D.W. Kicklighter, A.L. Grace, B. Morre III, and C.J. Vorosmarty. 1992. Interactions between carbon and nitrogen dynamics in estimating net primary productivity for potential vegetation in North America. Global Biogeochemical Cycles 6:101-124.

McGuire, A.D., L.A. Joyce, D.W. Kicklighter, J.M. Melillo, G. Esser, and C.J. Vorsomarty,. 1993. Productivity response of climax temperate forests to elevated temperature and carbon dioxide: a North American comparison between two global models. Climatic Change 24:287-310.

McIntyre, B.M, M.A. Scholl, and J.T. Sigmon. 1990. A quantitative description of a deciduous forest canopy using a photographic technique. Forest Science 36:381-393.

Medina, E. 1982. Physiological ecology of neotropical savanna plants. p. 308-336. *In* Ecology of Tropical Savannas. Ecological Studies 42. (B.J. Huntley and B.H. Walker, eds.) Springer-Verlag, New York.

Medina, E. and H. Klinge. 1983. Producitivity of tropical forests and tropical woodlands. p. 281-303. *In* Physiological Plant Ecology IV. Ecosystem Processes: Mineral Cycling, Productivity and Man's Influence. Encyclopedia of Plant Physiology New Series Volume 12D. (O.L. Lange, P.S. Nobel, C.B. Osmond, and H. Ziegler, eds.) Springer-Verlag, New York.

Meentemeyer, V., E.O. Box, and R. Thompson. 1982. World patterns and amounts of terrestrial plant litter production. Bioscience 32:125-128.

Meinzer, F., V. Seymour, and G. Goldstein. 1983. Water balance in developing leaves of four tropical savanna woody species. Oecologia (Berlin) 60:237-243.

Melillo, J.M., and J.D. Aber. 1984. Nutrient immobilization in decaying litter: an example of carbon-nutrient interactions. p. 193-215. *In* Trends in Ecological Research for the 1980s. (J.H. Cooley and F.B. Golley, eds.) Plenum, New York.

Melillo, J.M., A.D. McGuire, D.W. Kicklighter, B. Moore III, C.J. Vorosmarty, and A.L. Schloss. 1993. Global climate change and terrestrial net primary production. Nature 363:234-240.

Miller, R.B. 1961. The chemical composition of rainwater at Taita, New Zealand, 1956-1958. New Zealand Journal of Science 4:844-853.

Miller, R.B.1963a. Plant nutrients in hard beech. I. The immobilisation of nutrients. New Zealand Journal of Science 6:365-377.

Miller, R.B. 1963b. Plant nutrients in hard beech. III. The cycle of nutrients. New Zealand Journal of Science 6:388-413.

Miller, R.B. 1968. Flows and cycles of macro- and micro-elements in a forest soil and its environment. p.323-331. In 9th International Congress of Soil Science Transactions (Adelaide, Australia 1968) Vol IV. Int'l. Soc. of Soil Science and Angus and Robertson, Sydney, Australia.

Miller, R.B. and F.B. Hurst. 1957. The quantity and nutrient content of hard beech litter. New Zealand Forestry Research Notes 8:1-14.

Miller, P.C., W.A. Stoner, and J.R. Ehleringer. 1978. Some aspects of vascular plants of arctic and alpine regions. p. 343-357. *In* Vegetation and Production Ecology of an Alaskan Arctic Tundra. Ecological Studies 29. (L.L. Tieszen, ed.) Springer-Verlag, New York.

Miller, P.C., E. Hajek, D.K. Poole, S.W. Roberts. 1981. Microclimate and energy exchange. p. 97-121. *In* Resource Use by Chaparral and Matorral: A Comparison of Vegetation Function in Two Mediterranean Type Ecosystems.Ecological Studies 39. (P.C. Miller, ed.) Springer-Verlag, New York.

Miller, P.C., P.J. Webber, W.C. Oechel, and L.L. Tieszen. 1980. Biophysical processes and primary production. p.66-101. *In* An Arctic Ecosystem. The Coastal Tundra at Barrow, Alaska. US/IBP Synthesis Series 12. (J. Brown, P.C. Miller, L.L. Tieszen, and F.L. Bunnell, eds.) Dowden, Hutchinson, & Ross, Stroudsberg, Pennsylvania.

Miller, P.C., P.M. Miller, M. Blake-Jacobson, F.S. Chapin III, K.R. Everett, D.W. Hilbert, J. Kummerow, A.E. Likens, G.M. Marion, W.C. Oechel, S.W. Roberts, and L. Stuart. 1984. Plant-soil processes in *Eriophorium vaginatum* tussock tundra in Alaska: a systems modeling approach. Ecological Monographs 54:361-405.

Misra, R. 1972. A comparative study of net primary productivity of dry deciduous forest and grassland of Varanasi, India. p. 279-293. In Tropical Ecology with an Emphasis on Organic Productivity (P.M. Golley and F.B. Golley, eds.) University of Georgia, Athens, Georgia.

Misra, R. 1983. Indian savannas. p. 151-166. *In* Tropical Savannas. Ecosystems of the World 13. (F. Bourliere, ed.) Elsevier, New York.

Monson, R.K., M.R. Sackschewsky, and G.J. Williams, III. 1986. Field measurements of photosynthesis, water-use-efficiency, and growth in *Agropyron smithii* (C_3) and *Bouteloua gracilis* (C_4) in the Colorado shortgrass steppe. Oecologia (Berlin) 68:400-409.

Monteith, J.L., and M.H. Unsworth. 1990. Principles of Environmental Physics. 2nd ed. Edward Arnold, New York.

Mooney, H.A. 1988. Southern coastal shrub. p. 471-489. *In* Terrestrial Vegetation of California. Special Publication No. 9 (M.G. Barbour and J. Major, eds.) California Native Plant Society, Sacramento, CA.

Moore, T.R. 1980. The nutrient status of subarctic woodland soils. Arctic and Alpine Research 12:147-160.

Moore, L.B. and J.B. Irwin. 1978. The Oxford Book of New Zealand Plants. Oxford University Press, New York. 234 p.

Muller, M.J. 1982. Selected Climatic Data for a Global Set of Standard Stations for Vegetation Science. Dr. W. Junk, Boston. 306 p.

Munz, P.A. and D.D. Keck. 1963. A California Flora. University of California Press, Berkeley. 1681 p.

Murphy, P.G. and A.E. Lugo. 1986. Structure and biomass of a subtropical dry forest in Puerto Rico. Biotropica 18:89-96.

National Atmospheric Deposition Program (NRSP-3)/National Trends Network. NADP. 1995. NADP/NNTN Coordination Office, Natural Resource Ecology Laboratory, Colorado State University, Fort Collins, CO 80523.

National Climate Data Center (NCDC). 1995. Monthly precipitation data for U.S. Cooperative and National Weather Service sites. Alaska. Asheville, NC 28801.

Neftel, A., E. Moor, H. Oeschger, and B. Stauffer. 1985. Evidence from polar ice cores for the increasce in atmospheric CO_2 in the past two centuries. Nature 315:45-47.

New Zealand Meteorological Service. 1962. Meteorological Observations for 1959. Misc. Pub. 109. Government Printer, Wellington, New Zealand.

Ng, E. and R.S. Loomis. 1984. Simulation of growth and yield of the potato crop. Centre for Agricultureal Publishing and Documentation, Wagingen, Netherlands.147 p.

Nicholson, H.M. and T.R. Moore. 1977. Pedogenesis in a subarctic iron-rich environment: Schefferville, Quebec. Canadian Journal of Soil Science 57:35-35.

Nilsen, E.T., M.R. Sharifi, P.W. Rundel, W.M. Jarrell, and R.A. Virginia. 1983. Diurnal and seasonal water relations of the desert phreatophyte Prosopis glandulosa (honey mesquite) in the Sonoran Desert of California. Ecology 64:1381-1393.

NOAA. National Oceanic and Atmospheric Administration. 1974a. Climates of the States. Vol I-Eastern States. Water Information Center, Port Washington, New York.

NOAA. National Oceanic and Atmospheric Administration. 1974b. Climates of the States. Vol II-Western States. Water Information Center, Port Washington, New York.

Numata, M. 1979. Primary producers in meadows. p. 127-138. *In* Grassland ecosystems of the world: analysis of grasslands and their uses. International Biological Program 18. (R.T. Coupland, ed.) Cambridge University Press, New York.

Oberbauer, S.F. and W.C. Oechel. 1989. Maximum CO_2-assimilation rates of vascular plants on an Alaskan arctic tundra slope. Holarctic Ecology 12:312-316.

Oechel, W.C., S.J. Hastings, G. Vourlitis, M. Jenkins, G. Reichers, N. Grulke. 1993. Recent change of Arctic tundra ecosystems from a net carbon dioxide sink to a source. Nature 361:520-523.

Ojima, D.,ed. 1992. Modeling the Earth System. Global Change Institute Volume 3. UCAR/Office for Interdisciplinary Earth Studies, Boulder, CO. 488 p.

Osonubi, O. and W.J. Davis. 1980. The influence of plant water stress on stomatal control of gas exchange at different levels of atmospheric humidity. Oecologia (Berl.) 46:1-6.

Ovington, J.D., D. Heitkamp, and D.B. Lawrence. 1963. Plant biomasss and productivity of prairie, savanna, oakwood, and maize field ecosystems in central Minnesota. Ecology 44:52-63.

Parton, W.J., D.S. Schimel, C.V. Cole, and D.S. Ojima. 1987. Analysis of factors controlling soil organic matter levels in Great Plains grasslands. Soil Sci. Soc. Am. J. 51:1173-1179.

Peterjohn, W.T., J.M. Melillo, P.A. Steudler, K.M. Newkirk, F.P. Bowles, and J.D. Aber. 1994. Responses of trace gas fluxes and N availability to experimentally elevated soil temperatures. Ecological Applications 4:617-625.

Pittock, A.B. and H.A. Nix. 1986. The effect of changing climate on Australian biomass production-a preliminary study. Climatic Change 8:243-255.

Poole, D.K., S.W. Roberts, and P.C. Miller. 1981. Water utilization. p. 124-149. *In* Resource Use by Chaparral and Matorral: A Comparison of Vegetation Function in Two Mediterranean Type Ecosystems.Ecological Studies 39. (P.C. Miller, ed.) Springer-Verlag, New York.

Pooley, E. 1993. The Complete Field Guide to Trees of Natal, Zululand & Transkei. Natal Flora Publications Trust, Durban. 511 p.

Potter, C.S., J.T. Randerson, C.B. Field, P.A. Matson, P.M Vitousek, H.A. Mooney, and S.A. Klooster. 1993. Terrestrial ecosystem production: a process model based on global satellite and surface data. Global Biogeochemical Cycles 7:811-841.

Prance, G.T. 1990. The floristic compostion of the forests of central Amazonian Brazil. p.112-140. In Four Neotropical Rainforests (A.H. Gentry, ed.) Yale University Press, New Haven.

Pratt, G.C., E.J. Orr, D.C. Bock, R.L. Strassman, D.W. Fundane, C.J. Twaroski, and J.D. Thornton. 1995. Dry deposition of inorganics in Minnesota. Environmental Science and Technology submitted for publication.

Raich, J.W., E.B. Rastetter, J.M. Melillo, D.W. Kicklighter, P.A. Steudler, B.J. Peterson, A.L. Grace, B. Moore III, and C.J. Vorosmarty. 1991. Potential net primary production in South America. Ecological Applications 1:399-429.

Ramam, S.S. 1975. Primary production and nutrient cycling in tropical deciduous forest ecosystem. Tropical Ecology 16:140-146.

Rastetter, E.B. and G.R. Shaver. 1992. A model of multiple-element limitation for acclimating vegetation. Ecology 73:1157-1174.

Reich, P.B. and T.M. Hinckley. 1989. Influence of pre-dawn water potential and soil-to-leaf hydraulic conductance on maximum daily leaf diffusive conductance in two oak species. Functional Ecology 3:719-726.

Rencz, A.N. and A.N. Auclair. 1978. Biomass distribution in a subarctic *Picea mariana-Cladonia alpestris* woodland. Canadian Journal of Forest Research 8:168-176.

Rencz, A.N. and A.N. Auclair. 1980. Dimension analysis of various components of black spruce in subarctic lichen woodland. Canadian Journal of Forest Research 10:491-497.

Rhizopoulou, S. and K. Mitrakos. 1990. Water relations of evergreen sclerophylls. I. Seasonal changes in the water relations of eleven species from the same environment. Annals of Botany 65:171-178.

Ripley, E.A. and R.E. Redmann. 1976. Grassland. p. 351-398. *In* Vegetation and the Atmosphere. Volume 2. Case Studies. (J.L. Monteith, ed.) Academic Press, New York.

Ripley, E.A. and B. Saugier. 1978. Biophysics of a natural grassland: evaporation. Journal of Applied Ecology 15:459-480.

Risser, P.G. and W.J. Parton. 1982. Ecosystem analysis of the tallgrass prairie: Nitrogen cycle. Ecology 63:1342-1351.

Risser, P.G., E.C. Birney, H.D. Blocker, S.W. May, W.J. Parton, and J.A. Wiens. 1981. The True Prairie Ecosystem. US/IBP Synthesis Series 16. Hutchinson Ross Publ. Co, Stroudsberg, PA. 533 p.

Roberts, J., O.M.R. Cabral, and L.Ferreira de Aguiar. 1990. Stomatal and boundary-layer conductances in an Amazonian terra firme rain forest. Journal of Applied Ecology 27:336-353.

Robichaux, R.H., P.W. Rundel, L. Stemmermann, J.E. Canfield, S.R. Morse, and W.E. Friedman. 1984. Tissue water deficits and plant growth in wet tropical environments. p. 99-112. *In* Physiological Ecology of Plants in the Wet Tropics. Tasks for Vegetation Science 12. (E. Medina, H.A. Mooney, and C. Vazquez-Yanes, eds.) Dr. W. Junk Publishers, Boston.

Roy, J., E. Garnier, and L.E. Jackson. 1987. Response of two perennial grasses to water availability in different habitats related to successional change under Mediterranean climate conditions. p 175-190. *In* Plant Responses to Stress: Functional Analysis in Mediterranean Ecosystems. NATO ASI Series G: Ecological SciencesVol. 15. (J.D. Tenhunen, F.M. Catarino, O.L. Lange, and W.C. Oechel, eds.) Springer-Verlag, New York.

Running, S.W. 1984. Documentation and preliminary validation of H2OTRANS and DAYTRANS, two models for predicting transpiration and water stress in western coniferous forests. USDA Forest Service RM-252, Rocky Mountain Forest and Range Experiment Station, Fort Collins, CO.

Running, S.W. and J.C. Coughlan. 1988. A general model of forest ecosystem processes for regional applications. I. Hydrologic balance, canopy gas exchange, and primary production processes. Ecological Modelling 42:125-154.

Running, S.W. and E.R. Hunt, Jr. 1993. Generalization of a forest ecosystem process model for other biomes, BIOME-BGC, and an appliation for global-scale models. p. 141-158. *In* Scaling Physiological Process. Leaf to Globe (J.R. Ehleringer and C.B. Field, eds.) Academic Press, New York.

Sala, O.E., W.K. Lauenroth, and C.P.P. Reid. 1982. Water relations: a new dimension for niche separation between *Bouteloua gracilis* and *Agropyron smithii* in North American semi-arid grasslands. Journal of Applied Ecology 19:647-658.

Satoo, T. 1983. Temperate broad-leaved evergreen forests of Japan. p. 169-189. *In* Temperate Broad-leaved Evergreen Forest. Ecosystems of the World 10. (J.D. Ovington, ed.) Elsevier, New York.

Schlesinger, M.E. and J.F.B. Mitchell. 1987. Climate model simulations of the equilibrium climatic response to increased carbon dioxide. Reviews of Geophysics 25:760-798.

Schulze, E.-D. 1982. Plant life forms and their carbon, water, and nutrient relations. p. 615-676. *In* Physiologcial Plant Ecology II. Water Relations and Carbon Assimilation. Encyclopedia of Plant Physiology New Series Volume 12B. (O.L. Lange, P.S. Nobel, C.B. Osmond, and H. Ziegler, eds.) Springer-Verlag. New York.

Schulze, E.-D.and A.E. Hall. 1982. Stomatal responses, water loss, and CO_2 assimilation rates of plants in contrasting environments. p. 181-230. *In* Physiologcial Plant Ecology II. Water Relations and Carbon Assimilation. Encyclopedia of Plant Physiology New Series Volume 12B. (O.L. Lange, P.S. Nobel, C.B. Osmond, and H. Ziegler, eds.) Springer-Verlag. New York.

Schulze, E.-D. and M. Kuppers. 1979. Short-term and long-term effects of plant water deficits on stomatal response to humidity in *Corylus avellana* L. Planta 146:319-326.

Sharma, M.L. 1984. Evapotranspiration from a *Eucalyptus* community. p. 41-56. *In* Evapotranspiration from Plant Communities. Developments in Agricultural and Managed-Forest Ecosystems. (M.L. Sharma, ed.) Elsevier, New York.

Shaver, G.R. and F.S. Chapin, III. 1991. Production: biomass relationships, and element cycling in contrasting arctic vegetation types. Ecological Monographs 61:1-31.

Shreve, F. and I.L. Wiggins. 1964. Vegetation and Flora of the Sonoran Desert. Vol. I and II. Stanford University Press, Stanford, CA. 1740 p.

Sims, P.L. and R.T. Coupland. 1979. Producers. p. 49-72. *In* Grassland ecosystems of the world: analysis of grasslands and their uses. International Biological Program 18. (R.T. Coupland, ed.) Cambridge University Press, New York.

Sims, P.L., J.S. Singh, and W.K. Lauenroth. 1978. The structure and function of ten western North American grasslands. I. Abiotic and vegetational characteristics. Journal of Ecology 66:251-285.

Smith, S.D. and R.S.Nowak. 1990. Ecophysiology of plants in the intermountain lowlands. p. 180-241. *In* Plant Biology of the Basin and Range. Ecological Studies 80. (C.B.Osmond, L.F. Pitelks, G.M.Hidy, eds.) Springer-Verlag, New York.

Smith, T.M., R. Leemans, and H.H. Shugart. 1992. Sensitivity of terrestrial carbon storage to CO_2-induced climate change: comparison of four scenatios based on general circulation models. Climatic Change 21:367-384.

Smith, T.M. and H.H. Shugart. 1993. The transient response of terrestrial carbon storage to a perturbed climate. Nature 361:523-526.

Smith, W.K. and A.K.Knapp. 1990. Ecophysiology of high elevation forests. p. 87-142. *In* Plant Biology of the Basin and Range. Ecological Studies 80 (C.B.Osmond, L.F. Pitelks, G.M.Hidy, eds.) Springer-Verlag, New York.

Smith, W.K., D.R. Young, G.A. Carter, J.L. Hadley, and G.M. McNaughton. 1984. Autumn stomatal closure in six conifer species of the Central Rocky Mountains. Oecologia (Berlin) 63:237-242.

Sollins, P., C.C. Grier, F.M. McCorison, K. Cromack, Jr., R. Fogel, and R.L. Fredriksen. 1980. The internal element cycles of an old-growth Douglas-fir ecosystem in western Oregon. Ecological Monographs 50:261-285.

Steward, D. and P.J. Webber. 1981. The plant communities and their environment. p. 43-68. *In* Resource Use by Chaparral and Matorral: A Comparison of Vegetation Function

in Two Mediterranean Type Ecosystems.Ecological Studies 39. (P.C. Miller, ed.) Springer-Verlag, New York.

Swift, L.W., Jr. 1976. Algorithm for solar radiation on mountain slopes. Water Resources Research 12:108-112.

Szarek, S.R. and R.M. Woodhouse. 1976. Ecophysiological studies of Sonoran Desert plants. Oecologia (Berl.) 26:225-234.

Tans, P.P., I.Y. Fung, and T. Takahashi. 1990. Observational constraints on the global atmospheric CO_2 budget. Science 247:1431-1438.

Tanner, E.V.J. 1980. Studies on the biomass and productivity in a series of Montane Rain forests in Jamaica. Journal of Ecology 68:573-598.

Thom, A.S. 1975. Momentum, mass, and heat exchange of plant communities. p. 57-109. *In* Vegetation and the Atmosphere. Volume 1. Principles. (J.L. Monteith, ed.) Academic Press, New York.

Thornthwaite, C.W. and J.R. Mather. 1957. Instructions and tables for computing potential evapotranspiration and the water balance. Publications in Climatology 10(3). Drexel Institute of Technology, Centerton, NJ.

Turner, N.C. and G.H. Heichel. 1977. Stomatal development and seasonal changes in diffusive resistance of primary and regrowth foliage of red oak (*Quercus rubra* L.) and red maple (Acer rubrum L.). New Phytologist 78:71-81.

Turner, N.C., E.-D. Schulze, and T. Gollan. 1984. The responses of stomata and leaf gas exchange to vapour pressure deficits and soil water content. I. Species comparisons at high soil water contents. Oecologia (Berl.) 63:338-342.

Turton, S.M. 1986. Solar radiation under cloudless skies. Weatherwise 39:223-224.

Ullman, I., O.L. Lange, H. Ziegler, J. Ehleringer, E.-D. Schulze, and I.R. Cowan. 1985. Diurnal courses of leaf conductance and transpiration of mistletoes and their hosts in Central Australia. Oecologia (Berlin) 67:577-587.

Van Cleve, K., L. Oliver, R. Schlentner, L.A. Vierek, and C.T. Dyrness. 1983. Productivity and nutrient cycling taiga forest ecosystems. Canadian Journal of Forest Research 13:747-766.

Vasek, F.C. and M.B. Barbour. 1988. Mojave desert scrub vegetation. p. 835-868. *In* Terrestrial Vegetation of California (M.G. Barbour and J. Major, eds.) California Native Plant Society, Sacramento, California.

Viereck, L.A., C.T. Dyrness, K. Van Cleve, M.J. Foote. 1983. Vegetation, soils, and forest productivity in selected forest types in interior Alaska. Canadian Journal of Forest Research 13:703-720.

Vitousek, P.M., J.R. Gosz, C.C. Grier, J.M. Melillo, and W.A. Reiners. 1982. A comparative analysis of potential nitrification and nitrate mobility in forest ecosystems. Ecological Monographs 52:155-177.

Vorosmarty, C.J., B. Moore III, A.L. Grace, M.P. Gildea, J.M. Melillo, B.J. Peterson, E.B. Rastetter, and P.A. Steudler. 1989. Continental scale models of water balance and fluvial transport: an application to South America. Global Biogeochemical Cycles 3:241-265.

Wang, Y.S., D.R. Miller, J.M. Welles, and G.M. Heisler. 1992. Spatial variability of canopy foliage in an oak forest estimated with fisheye sensors. Forest Science 38:854-865.

Waring, R.H. and W. H. Schlesinger. 1985. Forest Ecosystems:Concepts and Management. Academic Press, New York. 340 p.

Waring, R.H., J.J. Rogers, and W.T. Swank.1981. Water relations and hydrologic cycles. p. 205-264. *In* Dynamic Properties of Forest Ecosystems. International Biological Programme 23. (D.E. Reichle, ed.) Cambridge University Press, New York.

Watts, W.R., R.E. Neilson, and P.G. Jarvis. 1976. Photosynthesis in Sitka spruce (*Picea sitchensis* (Bong.) Carr.). VII. Measurements of stomatal conductance and 14CO2 uptake in a forest canopy. Journal of Applied Ecology 13:623-638.

WeatherDisc Associates 1989. World WeatherDisc^{TM} User Manual.Seattle, WA. 38 p.

Weber, M.G. and K. Van Cleve. 1984. Nitrogen transformations in feather moss and forest floor layers of interior Alaska black spruce ecosystems. Canadian Journal of Forest Research 14:278-290.

Weinstein, D.A., R.D. Yanai, C.W. Chen, and L.E. Gomez. 1991. Models to Assess the Response of Vegetation to Global Change. EN-7366 Electric Power Research Institute, Palo Alto, CA. 16 p.

Welsh, S.L. 1974. Anderson's Flora of Alaska. Brigham Young University Press, Provo, Utah.

Whittaker, R.H. and W.A. Niering. 1975. Vegetation of Santa Catalina Mountains, Arizona. V. Biomass, production, and diversity along the elevation gradient. Ecology 56:771-790.

Woodmansee, R.G. 1979. Factors influencing input and output of nitrogen in grasslands. p. 117-134. In Perspectives in Grassland Ecology. Ecological Studies 32. (N.R. French, ed.) Springer-Verlag, New York.

Woodmansee, R.G., J.L. Dodd, R.A. Bowman, F.E. Clark, and C.E. Dickinson. 1978. Nitrogen budget of a shortgrass prairie ecosystem. Oecologia (Berl.) 34:363-376.

Table A.1. Synopsis of equations of TERRA categorized by submodel and process.

Submodel and Process, Definition, or Function	Equation number	Equation
Radiation submodel		
Solar declination for day *jd*	A.1	$\delta = -d_{cE}\cos[2\pi\,(jd+10)/365]\,\pi/180$
Sine of solar altitude	A.2	$\sin(\phi) = \sin(\mu\pi/180)\sin(\delta) +$ $\cos(\mu\pi/180)\cos(\delta)\cos[(\eta-12)\pi/12]$
Optical air mass	A.3	$m = 1/\sin(\phi)$
Instantaneous direct irradiance	A.4	$S_b = S_p\,\tau^m\,\sin(\phi)$
Instantaneous diffuse irradiance	A.5	$S_d = \alpha\,(\beta\,S_p\,\sin(\phi) - S_b)$
Total daily irradiance (cloudless sky)	A.6	$S_T = \int\limits_0^{24}(S_b + S_d)H\big[\sin(\phi)\big]d\eta \bullet 3600$
Heaviside function	A.7	$H(x) = \begin{cases} 1 & x \ge 0 \\ 0 & x < 0 \end{cases}$
Net daily radiation under cloudy skies	A.8	$R_n = [1 - al(v,ssn)]\,[c_1 + c_2\,sh(mo)]\,S_T$
Photosynthetically active radiation	A.9	$PAR = R_n\,\{sh(mo)\,cld_2 + [1 - sh(mo)]\,cld_1\}$
Leaf phenology submodel		
Algorithm for current leaf development as a fraction of maximum *lai*	A.10	INITIALIZE $k_{leaf}(1) = min_{leaf}(v)$ REPEAT
	A.11	$\text{k}_{leaf}(mo) = a_{leaf}(v)\,aet_T(mo)/aet_{Tmax} + b_{leaf}(v)\,k_{leaf}(mo-1) + c_{leaf}(v)$
	A.12	IF $[k_{leaf}(mo) > 1]$ THEN $k_{leaf}(mo) = 1$
	A.13	IF $[k_{leaf}(mo) < min_{leaf}(v)\,]$ THEN $kl_{eaf}(mo) = min_{leaf}(mo)$ UNTIL $k_{leaf}(mo) = k_{leaf}(mo + 12)$
	A.14	FOR ALL mo , $k_{leaf}(mo) \leftarrow k_{leaf}(mo)/kleaf_{max}$ where $kleaf_{max} = \text{maximum}(k_{leaf}(1),..., k_{leaf}(12))$
Thornthwaite heat index	A.15	$heati = \sum\limits_{mo=1}^{12}[T(mo)/5]^{1.514}$
Exponent for calculating Thornthwaite potential ET	A.16	$a_{TW} = 0.675 \bullet 10^{-6}heati^3 - 77.1 \bullet 10^{-6}heati^2 + 0.01792heati + 0.49239$
Thornthwaite potential ET	A.17	$pet_T(mo) = 16\big[10T(mo)/heati\big]^{a_{TW}}$
Soil water capacity	A.18	$\Theta_{fc} = fc_{sv}(s)rt(s,ir(v))$
Average daytime temperature	A.19	$T_{day}(mo) = 0.212\big[T_{d\max}(mo) - T(mo)\big] + T(mo)$
Average nighttime temp.	A.20	$T_{nt}(mo) = \big[T_{day}(mo) + T_{dmin}(mo)\big]/2$
Snowfall (Thornthwaite)	A.21	$snow_T(mo) = \begin{cases} p(mo) & T_{nt}(mo) \le 0 \\ 0 & T_{nt}(mo) > 0 \end{cases}$

Table A.1. (Continued)

Submodel and Process, Definition, or Function	Equation number	Equation
Rainfall (Thornthwaite)	A.22	$rain_T(mo) = \begin{cases} p(mo) & T_{nt}(mo) > 0 \\ 0 & T_{nt}(mo) \leq 0 \end{cases}$
Potential daily snowmelt	A.23	$snmlt = \max[T_{day}(mo)sncft, 0]$
Monthly snowmelt	A.24	$snmt_T(mo) = \min[snmlt \bullet jdtot(mo), snpk_T(mo)]$
Snowpack dynamics	A.25	$snpk_T(mo) = snpk_T(mo-1) + snow_T(mo) - snmt_T(mo)$
Coefficient of decay of water in soil under 'dry' conditions	A.26	$a_{slw} = \dfrac{\ln(1000\ \Theta_{fc})}{(1128.2\ \Theta_{fc})^{1.2756}}$
Change of water in soil for 'dry' or 'wet' conditions	A.27	$\Delta_{swT}(mo) = \begin{cases} -\Theta_T(mo) \bullet \\ \left\{1 - e^{-a_{slw}[pet_T(mo)-rain_T(mo)-snmt_T(mo)]}\right\} \\ \quad \text{for}[rain_T(mo) + snmt_T(mo)] \\ \qquad < pet_T(mo) \quad (\Rightarrow' \text{dry}') \\ \min\begin{bmatrix} snmt_T(mo) + rain_T(mo) \\ -pet_T(mo), \Theta_{fc} - \Theta_T(mo) \end{bmatrix} \\ \text{for}[rain_T(mo) + snmt_T(mo)] \\ \qquad \geq pet_T(mo) \quad (\Rightarrow' \text{wet}') \end{cases}$
New soil moisture from water conservation	A.28	$\Theta_T(mo) = \Theta_T(mo-1) + \Delta_{swT}(mo)$
Actual evapotranspiration (Thornthwaite)	A.29	$aet_T(mo) = \begin{cases} snmt_T(mo) + rain_T(mo) - \Delta_{swT}(mo) \\ \quad\quad \text{if ' dry'} \\ pet_T(mo) \quad\quad\quad\quad\quad \text{if ' wet'} \end{cases}$

Water balance submodel

Submodel and Process, Definition, or Function	Equation number	Equation
Soil water at the wilting point	A.30	$\Theta_{wp} = wp_{sv}(s)\, rt(s, ir(v))$
Coefficient to convert soil water content to soil water potential	A.31	$w_{co} = e^{\ln\left[\frac{(-\Psi_w)^{\ln(\Theta_{fc})}}{(-\Psi_f)^{\ln(\Theta_{wp})}}\right] / \ln\left(\Theta_{fc}/\Theta_{wp}\right)}$
Exponent to convert soil water content to soil water potential	A.32	$w_{ex} = \dfrac{\ln(\Psi_f / \Psi_w)}{\ln(\Theta_{fc}/\Theta_{wp})}$
Leaf area index	A.33	$lai = lai_{\max}(v)\, k_{leaf}(mo)$
Soil temperature	A.34	$tsoil = \begin{cases} T(mo) & snpk(jd) = 0 \\ 0 & snpk(jd) > 0 \end{cases}$
Saturation vapor pressure during the day	A.35	$e_s = 0.61078\, e^{17.269\, T_{day}(mo)/[237.2 + T_{day}(mo)]}$

Table A.1. (Continued)

Submodel and Process, Definition, or Function	Equation number	Equation
Vapor pressure	A.36	$e_v = 0.61078 e^{17.269 dewpt(mo)/[237.2+dewpt(mo)]}$
Vapor pressure deficit	A.37	$vpd = \max(e_s - e_v, 0)$
Absolute humidity deficit	A.38	$ahd = \dfrac{2165 vpd}{T_{day}(mo) + 273.2}$
Daylength	A.39	$dayl = \dfrac{73440}{\pi} \arccos$ $\left(\max\left\{ \min\left[1, -\tan(\mu\,\pi/180)\tan(\delta + 0.4\pi/180)\right], -1 \right\} \right)$
Radiation absorbed by canopy	A.40	$R_{dcan} = R_n \left[1 - e^{-lai\,k_{can}(v)/p_l(v)} \right]$
Average radiation in the canopy	A.41	$R_{avc} = {R_{dcan}} \Big/ {\left[lai\ k_{can}(v)/p_l(v) \right]}$
Rain on rainy days	A.42	$rain(jd) = \begin{cases} p(mo)/nrd(mo) - lai\ c_{ip}(v) \\ \qquad\qquad\qquad T_{nt}(mo) > 0 \\ 0 \qquad\qquad\qquad T_{nt}(mo) \le 0 \end{cases}$
Snow on snowy days	A.43	$snow(jd) = \begin{cases} p(mo)/nrd(mo) & T_{nt}(mo) \le 0 \\ 0 & T_{nt}(mo) > 0 \end{cases}$
Snowmelt	A.44	$snmlt_D(jd) = \max\left[snmlt, snpk(jd) \right]$
Possible evaporation from intercepted precipitation on rainy days	A.45	$pe(jd) = p(mo)/nrd(mo) - rain(jd) - snow(jd)$
Limit on evaporation due to radiation	A.46	$pre = R_n/2.5 \bullet 10^9$
Excess canopy interception	A.47	$eclf = \max\left[pe(jd) - pre, 0 \right]$
Actual evaporation	A.48	$ae(jd) = \min\left[pe(jd), pre \right]$
Soil water potential	A.49	$\Psi'_s = -w_{co} \Theta(jd)^{w_{ex}}$
Soil water potential corrected for cold soil temperatures	A.50	$\Psi_s = \begin{cases} cldsoil\ \Psi'_s & v \le 4\ \text{or}\ tsoil \le 0 \\ \Psi'_s & v > 4\ \text{and}\ tsoil > 0 \end{cases}$
Canopy conductivity	A.51	$cd = cn_{slw}(\Psi_s)\, cn_{tp}\left(T_{d\min}(mo), T_{day}(mo) \right) \bullet$ $cn_{hm}(ahd)\, cn_{lt}(R_{avc})$
Dependence of conductivity on soil water potential	A.52	$cn_{slw}(\Psi_s) = \max$ $\left\{ \min\left[cn_{max}(v), cn_{max}(v)\left(1 - \dfrac{\left|\Psi_f\right| - \left|\Psi_s\right|}{\left|\Psi_f\right| - \left|\Psi_w\right|} \right) \right], 0.00005 \right\}$

Table A.1. (Continued)

Submodel and Process, Definition, or Function	Equation number	Equation
Dependence of conductivity on temperature	A.53	$$cn_{tp}\left(T_{dmin}, T_{day}\right) = \begin{cases} 1 + \dfrac{s_{nt}(v)T_{dmin}(mo)}{cn_{slw}(\Psi_s)} \\ \qquad\qquad\qquad T_{dmin}(mo) < 0 \\ 1 + s_{td}(v)\left[T_{day}(mo) - T_{tcd}(v)\right] \\ \qquad\qquad\qquad T_{dmin}(mo) \ge 0 \end{cases}$$
Dependence of conductivity on absolute humidity deficit	A.54	$cn_{hm}(ahd) = \min\left(1, 1 - s_{ahd}(v)\left[ahd - ahd_t(v)\right]\right)$
Dependence of conductivity on light	A.55	$cn_{lt}(R_{avc}) = \min\left[1, R_{avc}/R_{thr}(v)\right]$
Canopy transpiration function: Penman-Monteith equation	A.56	$penmon\left(T_{day}, vpd, R_{dcan}, cd, dayl\right) =$ $$\dfrac{slp\left(T_{day}\right)crad\left(R_{dcan}, dayl\right) + c_p\rho_a\dfrac{vpd}{r_a}\dfrac{lai}{2}}{xlat\left(T_{day}\right)\left\{slp\left(T_{day}\right) + \gamma\left(T_{day}\right)\left[1 + \dfrac{r_s(cd)}{r_a}\right]\right\}}$$
Stomatal resistance	A.57	$r_s(cd) = 1/cd$
Slope of saturation vapor pressure curve with respect to temperature	A.58	$slp(T) = \dfrac{d}{dT}e_s(T)$
Average daily radiation absorbed in canopy	A.59	$crad = R_{dcan}/dayl$
Density of air	A.60	$\rho_a\left(T_{day}\right) = 1.292 - 0.00428\ T_{day}$
Latent heat of vaporization of water	A.61	$xlat = \left(2.501 - 0.0024T_{day}\right)10^6$
Psychrometer constant	A.62	$\gamma = 0.646 + 0.0006\ T_{day}$
Potential transpiration for day	A.63	$pt(jd) = penmon\left(T_{day}, vpd, R_{dcan}, cn_{max}(v), dayl\right)\ dayl$
Actual transpiration for day	A.64	$at(jd) = penmon\left(T_{day}, vpd, R_{dcan}, cd, dayl\right)\ dayl$
Runoff for day jd	A.65	$RO(jd) = \Theta(jd) - \Theta_{fc} + rain(jd) + snmlt_D(jd) + eclf$
Change in snowpack for day jd	A.66	$\Delta_{snD}(jd) = snow(jd) - snmlt_D(jd)$
Change in soil water for day jd	A.67	$\Delta_{swD}(jd) = rain(jd) + snmlt_D(jd) + eclf -$ $\qquad\qquad\qquad RO(jd) - at(jd)$
New snowpack	A.68	$snpk(jd+1) = snpk(jd) + \Delta_{snD}(jd)$
New soil water content	A.69	$\Theta(jd+1) = \Theta(jd) + \Delta_{swD}(jd)$
New cumulative runoff	A.70	$W_{RO}(jd+1) = W_{RO}(jd) + RO(jd)$
New cumulative transpiration	A.71	$W_{trn}(jd+1) = W_{trn}(jd) + at(jd)$
New cumulative evaporation	A.72	$W_{evp}(jd+1) = W_{evp}(jd) + ae(jd)$

Table A.1. (Continued)

Submodel and Process, Definition, or Function	Equation number	Equation
Carbon submodel		
Conversion of external CO_2 to internal leaf CO_2	A.73	$C_i = C_a\left[c_{if} + \left(1 - c_{if}\right)\dfrac{at(jd)}{pt(jd)}\right]$
Gross primary productivity	A.74	$gpp = C_{max}\dfrac{PAR}{PAR + k_{lgt}}\dfrac{C_i}{C_i + k_{CO_2}}f_T\big(T(mo)\big)\bullet$ $k_{leaf}(mo)\ ac$
Response of GPP to temperature	A.75	$f_T(T) = \begin{cases} \dfrac{\left[T - T_{min}(v)\right]\left[T - T_{max}(v)\right]}{\left[T - T_{min}(v)\right]\left[T - T_{max}(v)\right] - \left[T - T_{opt}(v)\right]^2} & \\ & T_{min}(v) \le T \le T_{max}(v) \\ 0 & T < T_{min}(v),\ T_{max}(v) < T \end{cases}$
Maintenance respiration	A.76	$r_m\big(T(mo)\big) = K_r(v)\ Q_{10}^{T(mo)/10}\ C_v$
Growth respiration	A.77	$r_g = \begin{cases} r_{grfc}\big(gpp - r_m\big) & gpp > r_m \\ 0 & gpp \le r_m \end{cases}$
Carbon transfer by litterfall	A.78	$L_c = C_v\ K_{fall}(v)$
Soil water as percent of saturation	A.79	$M = \dfrac{100\ \Theta(jd)}{pv_{sv}(s)\ rt\big(s, ir(v)\big)}$
Exponent in effect of moisture on decomposition	A.80	$B = \left[\dfrac{M^{ml(s)} - m_{opt}(s)^{ml(s)}}{m_{opt}(s)^{ml(s)} - 100^{ml(s)}}\right]^2$
Effect of moisture on decomposition	A.81	$moist = \big(1 - mst_{mn}\big)msat(s)^B + mst_{mn}$
Decomposition respiration	A.82	$r_H\big(T(mo)\big) = C_s\ K_d\ Q_{10}^{T(mo)/10}\ moist$
Net primary production	A.83	$npp = gpp - r_m - r_g$
Net ecosystem production	A.84	$nep = npp - r_H$
Rate of change of carbon in vegetation	A.85	$\dfrac{dC_v}{dt} = gpp - r_m - r_g - L_c$
Rate of change of carbon in soil	A.86	$\dfrac{dC_s}{dt} = L_c - r_H$
Nitrogen submodel		
Availability of nitrogen by way of diffusion in soil	A.87	$K_s = \big(1 - K_{min}\big)\left[M / fc_{sat}(s)\right]^3 + K_{min}$
Uptake of nitrogen by vegetation	A.88	$N_{pl} = N_{max}\ Q_{10}^{T(mo)/10}(1 - ac)\dfrac{K_s\ N_{av}}{K_s\ N_{av} + k_{n1}}$

Table A.1. (Continued)

Submodel and Process, Definition, or Function	Equation number	Equation
Gross mineralization of nitrogen	A.89	$G_{MN} = \dfrac{N_s}{C_s} r_H$
Immobilization of soil nitrogen by soil bacteria	A.90	$I_{MN} = \dfrac{N_{up} K_s N_{av}}{k_{n2} + K_s N_{av}} D\ r_H$
Annual decay rate to determine the state of the litter undergoing immobilization of nitrogen	A.91	$k_{lit} = k_{lsr}(v) K_d \displaystyle\int_0^1 Q^{T/10}\ moist\ dt$
Mean decay state of the active litter as affecting immobilization	A.92	$D = \dfrac{1}{6} \displaystyle\sum_{y=1}^{6} e^{-k_{lit}y}$
Net mineralization of nitrogen	A.93	$N_{min} = G_{MN} + I_{MN}$
Loss of nitrogen from plants to soil by litterfall	A.94	$L_n = L_c\left(N_v/C_v\right) V_{cn}(v) L_{nc}(v)$
Loss of nitrogen from soil	A.95	$\Delta_{NL} = N_{av} N_{loss}(v)$
Rate of change of nitrogen in vegetation	A.96	$\dfrac{dN_v}{dt} = N_{pl} - L_n$
Rate of change of organic nitrogen in soil	A.97	$\dfrac{dN_s}{dt} = L_n - N_{min}$
Rate of change of inorganic nitrogen in soil	A.98	$\dfrac{dN_{av}}{dt} = N_{input} \dfrac{365 p(mo)}{jdtot(mo)\sum_i p(i)} + N_{min} - N_{pl} - \Delta_{NL}$

Allocation submodel

Submodel and Process, Definition, or Function	Equation number	Equation
Relative allocation of resources to carbon *vs* nitrogen	A.99	$\dfrac{d\,ac}{dt} = adapt\,\dfrac{V_{cn}(v)N_v - C_v}{V_{cn}(v)N_v + C_v}$

Table A.2. Glossary of symbols used in calculating aerodynamic resistance to water vapor exchange between leaves in the canopy and a reference height above the canopy.

Symbol	Description	Equation	Units
d_h	Displacement height	A.102-A.108	m
D_L	Measured width of the leaf in the direction of the wind	A.108	m
H_v	Height of the vegetation	A.100 A.102-A.108	m
k_{vK}	Von Karman's constant	A.105	
r_{al}	Aerodynamic resistance of the leaf boundary layer	A.108, A.109	s m^{-1}
r_{acd}	Aerodynamic resistance to water vapor transfer from the discplacement height within the canopy to the top of the canopy	A.107 A.109	s m^{-1}
r_{pbl}	Aerodynamic resistance to water vapor transfer from the top of the canopy to the reference height z.	A.106 A.109	s m^{-1}
$u(h)$	Windspeed at height h above the ground	A.103 A.104 A.107 A.108	m s^{-1}
u^*	Friction velocity	A.105 A.107	m s^{-1}
W_L	Measured length of leaf perpendicular to the wind	A.108	m
z	Distance from the top of the canopy to the reference height[a].	A.103 A.105 A.106	m
z_{oM}	Roughness length for momentum transfer	A.100 A.101 A.103 A.106	m
z_{ov}	Roughness length for water vapor transfer	A.101 A.106	m

[a]Assumed to be the 6 m standard for meteorological towers.

Table A.3. Equations for calculating aerodynamic resistance.

Process or variable	Equation number	Equation
Roughness length for momentum transfer	A.100	$z_{oM} = 0.123 H_v$
Roughness length for water vapor transfer	A.101	$z_{ov} = 0.1 z_{oM}$
Displacement height	A.102	$d_h = \begin{cases} \dfrac{2}{3} H_v & Short\ systems \\ 0.78 H_v & Tall\ systems \end{cases}$
Windspeed at the canopy top	A.103	$u(H_v) = u(H_v + z) \dfrac{\ln\left[\dfrac{H_v - d_h}{z_{oM}}\right]}{\ln\left[\dfrac{H_v + z - d_h}{z_{oM}}\right]}$
Windspeed at the displacement height	A.104	$u(d_h) = u(H_v) e^{-3(1 - d_h / H_v)}$
Friction velocity	A.105	$u^* = k_{vK} \dfrac{u(H_v + z)}{\ln\left(\dfrac{H_v + z - d_h}{z_{oM}}\right)}$
Aerodynamic resistance to water vapor transfer from the top of the canopy to the reference height	A.106	$r_{pbl} = \dfrac{1}{k_{vK}^2 u(H_v + z)} \ln\left(\dfrac{H_v + z - d_h}{z_{oM}}\right) \ln\left(\dfrac{H_v + z - d_h}{z_{ov}}\right)$
Aerodynamic resistance to water vapor transfer from the displacement height to the top of the canopy	A.107	$r_{acd} = \dfrac{u(H_v) - u(d_h)}{u^*}$
Aerodynamic resistance of the leaf boundary layer	A.108	$r_{al} = 180 \dfrac{0.65^{0.55} D_L^{0.35} W_L^{0.2}}{u(d_h)^{0.55}}$
Total aerodynamic resistance	A.109	$r_a = r_{pbl} + r_{acd} + r_{al}$

Table A.4. Parameters and variables used in calculating aerodynamic resistance, r_a. Units are given in Table A.2.

Vegetation type	H_v	D_L	W_L	$u(H_v + z)$
Polar desert/alpine tundra	0.09[a]	0.005[k]	0.014	4.1
Wet/moist tundra	0.23[b]	0.003[l]	0.055	4.1
Boreal woodland	8.5[c]	0.001[m]	0.013	4.1
Boreal forest	12.7[d]	0.001[n]	0.009	2.8
Temperate coniferous forest	32.5[e]	0.002[o]	0.066	3.4
Arid shrubland	1.6[f]	0.005[p]	0.016	3.9
Short grassland	0.5[e]	0.002[q]	0.099	4.6
Tall grassland	1.0[e]	0.004[q]	0.228	5.8
Temperate savanna	9.5[g]	0.034[r]	0.139	4.8
Temperate deciduous forest	23[e]	0.069[s]	0.102	4.5
Temperate mixed forest	23[e]	0.024[t]	0.078	4.5
Temperate broadleaved evergreen forest	19[e]	0.027[u]	0.038	5.2
Mediterranean shrubland	2.9[h]	0.014[v]	0.034	2.9
Tropical savanna	4.8[i]	0.010[w]	0.120	3.1
Xeromorphic woodland	6.5[j]	0.024[x]	0.072	2.9
Tropical deciduous forest	31[d,e]	0.106[y]	0.137	1.9
Tropical evergreen forest	47[e]	0.058[z]	0.138	1.6

[a](Schulze1982, Shaver and Chapin 1991), [b](Lewis and Callaghan 1976, Miller et al. 1980, Chapin and Shaver 1985, Shaver and Chapin 1991), [c]Rencz and Auclair 1980, [d]DeAngelis et al. 1981, [e]Schulze 1982, [f](Schulze 1982, Vasek and Barbour 1988), [g]Ovington et al. 1963, [h]Hanes 1988, [i]Huntley and Morris 1982, [j]Lugo et al. 1978, [k](Shaver and Chapin 1991, Welsh 1974), [l](Shaver and Chapin 1991, Brown et al. 1980, Welsh 1974), [m](McGuire et al. 1992, Rencz and Auclair 1978, Welsh 1974, Harlow and Harrar 1969), [n](Van Cleve et al. 1983, Harlow and Harrar 1969, Welsh 1974), [o](Grier and Logan 1977, Harlow and Harrar 1969), [p](Caldwell et al. 1977, Vasek and Barbour 1988, Burk 1988, Shreve and Wiggins 1964, Munz and Keck 1963), [q](Risser et al. 1981, McGregor et al. 1986), [r](Ovington et al. 1963, McGregor et al. 1986), [s](Bowden et al. 1991, Harlow and Harrar 1969), [t](McGuire et al 1992, Harlow and Harrar 1969), [u](Miller 1963, Moore and Irwin 1978), [v](Steward and Webber 1981, Hanes 1988, Munz and Keck 1963), [w](Huntley and Morris 1982, Gibbs-Russell 1990, Pooley 1993, Keay 1989), [x](Lugo et al. 1978, Long and Lakela 1971), [y](Ramam 1975, Hooker 1875), [z](Prance 1990, Gentry 1993, Maas and Westra 1993)

Table A.5. Values of parameters determined by calibration as outlined in the text. Units are given in Table 1.

No. of System	Vegetation type	C_{max}	K_r	K_{fall}	K_d	N_{max}	L_{nc}	N_{up}	N_{loss}
1	Polar desert/ alpine tundra	5615.5	0.42122	0.14444	0.013956	4.3270	0.0076923	-0.19825	0.12500
2	Wet/moist tundra	9893.2	0.43549	0.16000	0.0088739	7.1265	0.0066667	-0.25879	0.12500
3	Boreal woodland	7212.0	0.10087	0.077273	0.029490	8.9010	0.0088235	-0.09001	0.04600
4	Boreal forest	8641.1	0.023851	0.024444	0.032517	19.939	0.010455	-0.25893	0.28986
5	Temperate coniferous forest	16757	0.017660	0.012299	0.018346	11.645	0.0078505	-0.07934	0.53333
6	Arid shrubland	4815.0	0.089386	0.20370	0.011590	8.7780	0.024545	-0.22934	0.30000
7	Short grassland	5166.4	0.19704	0.63492	0.060089	9.6830	0.017500	-1.2918	0.30000
8	Tall grassland	10851	0.18454	0.65385	0.0077846	4.2282	0.012941	-0.30540	0.25000
9	Temperate savanna	10770	0.075262	0.21429	0.063041	7.8490	0.012222	-1.0417	0.12093
10	Temperate deciduous forest	15496	0.018656	0.041935	0.037065	13.283	0.012308	-0.37284	0.30000
11	Temperate mixed forest	15321	0.028305	0.043919	0.040587	11.229	0.010000	-0.43658	0.30000
12	Temperate broadleaved evergreen forest	13979	0.026030	0.056667	0.031373	11.306	0.0070588	-0.46445	0.50000
13	Mediterranean shrubland	9677.2	0.039203	0.12881	0.0078707	6.1082	0.025455	-0.35370	0.038000
14	Tropical savanna	12215	0.099313	0.29795	0.043308	18.363	0.022988	-0.46484	0.35000
15	Xeromorphic woodland	10824	0.039260	0.12881	0.007862	5.8917	0.025455	-0.34075	0.038000
16	Tropical deciduous forest	19030	0.023043	0.062780	0.028054	14.542	0.038571	-1.3604	0.30000
17	Tropical evergreen forest	15601	0.012996	0.046667	0.011466	18.197	0.022857	-0.74575	2.0000